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Cover photo: Aggregation of offspring with mother whip spider, *Damon diadema* (Amblypygi, Phrynichidae). Photo by Linda S. Rayor.

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MATING IN THE ABSENCE OF VISUAL CUES BY *SCHIZOCOSA OCREATA* (HENTZ 1844) WOLF SPIDERS (ARANEAE, LYCOSIDAE)

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ABSTRACT. Male *Schizocosa ocreata* (Hentz 1844) wolf spiders court females with multi-modal displays that include both seismic and visual components. The seismic components are thought to be ancestral whereas the visual components are thought to have been more recently derived. We here present evidence that, despite the evolution of elaborate visual display components in males, female *S. ocreata* remain able to derive sufficient information about males through the seismic display components alone. We compared the mating tendency of females courted by males in the light (seismic and visual components present) and in the dark (only seismic components present). With a sample of 79 pairs in each condition, pairs were not significantly less likely to mate when in the dark (62%) than when in the light (73%). While all males performed courtship, and latency from the release of males until the onset of courtship was similar in the light and in the dark, latency until mounting tended to be much longer in the dark. This may mean that it takes longer for females to gather the information required to accept a male in the absence of visual cues or may instead simply reflect the challenge of locating mates and orienting for mounting. Lighting conditions did not influence how long the male remained mounted, indicating that these wolf spiders lack the condition-dependent flexibility in copula duration that is found in some jumping spiders.

Keywords: Multimodal signalling, vision, Lycosidae

Spiders have provided valuable models for recent studies into the function and evolution of "multi-modal communication" (sensu Partan & Marler 1999). In particular, the wolf spider genus *Schizocosa* Chamberlin 1904 (Lycosidae) has been widely adopted as a productive model system. *Schizocosa* vary in their use of seismic and visual displays in courtship communication, ranging from stationary palpal stridulation with little detectable movement through to combinations of stridulation and percussion along with extravagant raising and waving of ornamented legs (Uetz 2000; Stratton 2005). Seismic signalling appears to be ancestral, and is used by all *Schizocosa* species regardless of whether they also have visual display components (Stratton 2005). On the other hand, dynamic and morphological visual signalling components are observed in only a subset of *Schizocosa* species and appear to have evolved more recently (McClintock & Uetz 1996; Hebets & Uetz 1999; Uetz 2000; Stratton 2005).

One of the key questions in studies of multi-modal communication is of the extent to which each modal component contributes to receiver responses. Recently, Hebets (2005) investigated the extent to which the male visual and seismic courtship components are required for female acceptance in *S. uetzi* Stratton 1997, a species with only rudimentary visual displays. During courtship, male *S. uetzi* stand stationary while stridulating with their pedipalps. Their forelegs have darkened midtibiae and, while stridulating, they intermittently raise their forelegs in a slow arch (Stratton 1997). Hebets (2005) found that pairs were similarly likely to mate in the dark (visual components occluded) as in the light (visual components present), as long as the seismic components were present. That is, the evolution of visual display components in this species appears not to have extinguished their ability to interact and make mating decisions when limited to the ancestral seismic components alone. Is this also the case in *Schi-*

zocosa species with more developed visual display components?

Compared with *S. uetzi*, *S. ocreata* (Hentz 1844) has much more elaborate dynamic visual elements in its courtship and more elaborate morphological modifications that are thought to enhance detection of signals (Uetz & Denterlein 1979; Stratton & Uetz 1981, 1983, 1986; Uetz 2000; Taylor et al. 2005). Two quite different seismic components are produced along with visual displays; percussion is produced by rapidly "jerking" the body downward to strike the substrate, and strong bursts of stridulation are produced by specialized organs in the pedipalps as the spiders display visually by moving their forelegs up and down. Males have dark forelegs bearing large tufts and in several studies females have shown greater receptivity toward males with large tufts (McClintock & Uetz 1996; Scheffer et al. 1996; Uetz 2000; Persons & Uetz 2005).

In this study, we investigate how often the seismic courtship component alone provides sufficient information for *S. ocreata* females to accept males as mates. From an evolutionary perspective, we are hence asking about the extent to which these spiders have come to depend on the secondarily added visual display components. If females are usually able to obtain all the information they need to accept males as mates even when the visual signalling component is altogether absent, we should find similar mating tendency in the light and in the dark. On the other hand, if the visual mode provides necessary information, we should find a marked reduction in mating tendency of pairs in the dark. In addition to considering the female's decision of whether to accept the male as a mate, we also consider other measures of male sexual success, including latency until mounting from the start of trials and from the onset of courtship, and how long the male remained mounted.

Sub-adult males and females of *S. ocreata* were collected from dense leaf litter at Cincinnati Nature Center, Rowe Woods (Clermont County, Ohio, USA: 39°07.556′N, 84° 15.059′W), during March, April, May and September 2001. We kept spiders visually isolated from each other in white cylindrical plastic cages (11 cm diameter, 8.5 cm high) under laboratory conditions of 13:11 L:D photoperiod, ~23 °C and ~65% RH. Spiders were fed 2–3 crickets twice weekly and had continual access to water by way of a soaked cotton wick inserted through a hole in the cage floor into a reservoir below. Spiders matured in the laboratory and were used in experiments between 7 and 50 days after maturing. All spiders were virgins when tested.

Mating trials were carried out in open plastic boxes (150 × 100 × 50 mm, lwh) during the laboratory light phase (which corresponded closely with daylight), excluding the first and last two hours. In nature, we have often seen *S. ocreata* courtship taking place in dark places (e.g., in dense leaf litter under forest canopy) during the day. Since all trials were run at the same period of the day, we controlled for possible biorhythms in the behavior of the spiders. A clean piece of 5 mm thick foam-core board covered the floor. This material allows excellent transmission of vibrations. A thin film of Vaseline® petroleum jelly prevented spiders from climbing out of the box. A new piece of foam-core board was used in each trial, and the plastic box was washed with warm soapy water and 70% ethanol between trials to remove any silk and chemical cues. All trials were carried out in a photographic darkroom. For trials in the light, illumination was provided by two 25 W fluorescent lights suspended 0.5 m above the arena (mean 87.8 ± SE 1.3 lx). For trials in the dark (no detectable visible light), illumination was provided by an Infra-Red (IR) light source (Sony HVL-IRC). Wolf spider eyes are not sensitive to IR light (DeVoe 1972, summarized in Yamashita 1985) and so this setup is equivalent to total darkness for the spiders. All trials were video-recorded using an IR-sensitive camera (Watec WAT-902C) positioned above the testing arena, which was connected to the video input of a VHS VCR (Sony DA Pro 4 head).

Virgin females were released into the arena 1 h before males. During this hour, males were kept in the light conditions under which the trial was to be carried out. Males were then transferred into the testing arena from maintenance cages by the use of a 10 ml plastic vial. Pairs were left to interact for two hours after which un-mounted pairs were returned to their home cages. Mounted pairs were video-recorded until they separated naturally. There were no incidences of sexual cannibalism either in the light or in the dark.

Effects of light regime on the probability of mating were investigated by log-likelihood ratio (G). Effects of light regime on latency from male release until onset of courtship, latency from male release until mounting, latency from onset of courtship until mounting, and how long the male was mounted ("mount duration") were analyzed by Wilcoxon two-sample tests, using approximation to the normal distribution z (none of these data sets were normally distributed or of equal variance). All analyses were carried out using JMP v5 (SAS Institute).

With a sample size of 79 trials in each condition, pairs of *S. ocreata* wolf spiders were not significantly less likely to mate when in the dark (seismic display component only) than when in the light (visual + seismic display components available). Mounting and copulation was recorded within the 2-h testing period in 58 (73%) trials in the light and 49 (62%) trials in the dark ($n = 158$, $G_1 = 2.354$, $P = 0.125$). In previous studies, female *S. ocreata* have given "receptivity displays" to unseen courting males in adjacent chambers that occlude visual contact but allow transmission of seismic signals (Scheffer et al. 1996; Uetz 2000). Results of this study of direct interactions are consistent with results of these previous studies of female responses to males in adjacent chambers, indicating that female *S. ocreata* are usually able to obtain whatever information they need about a male through the seismic components of multimodal signals alone. Our results for *S. ocreata* are also very similar to those for *S. uetzi* by Hebets (2005), who found no evidence of reduced mating tendency when trials were run in darkness.

While choice of minor display elements and non-display behavior may vary slightly depending on whether *S. ocreata* males are courting in the dark or in the light, major display elements are performed similarly and the visual and seismic components of each display element are both retained regardless of lighting conditions (Taylor et al. 2005). The close synchrony of visual and seismic signalling components in *S. ocreata* means that display rates in these modes are tightly linked. In some wolf spiders, display rate is a key male attribute on which females base mating decisions (Kotiaho et al. 1996; Parri et al. 1997). If females of *S. ocreata* are also interested primarily in male display rate, then they may gain sufficient information regardless of whether the visual display components are present.

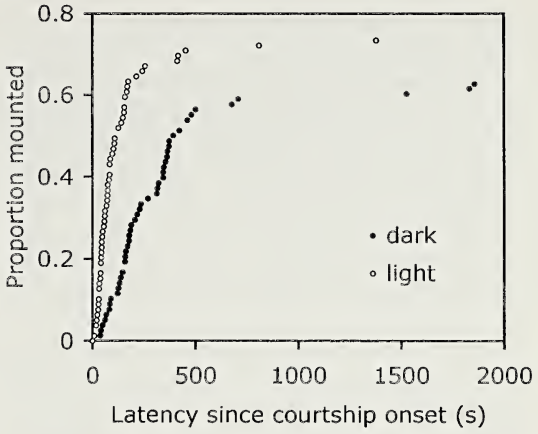

Figure 1.—Cumulative proportion of spiders mounted over time after the onset of courtship. The last spider to mount in the light was at 1378 s after the male began courting (1407 s after the male was released); the last in the dark was at 1857 s after the male began courting (1898 s after the male was released).

All tested males performed the major courtship element of "jerky tapping" (Stratton & Uetz 1981, 1983, 1986) during trials, regardless of whether they succeeded in mounting the female. Latency from release of the male until the onset of courtship did not vary between the dark (median = 22 s, range = 1–551 s) and in the light (median = 28 s, range = 2–415 s) ($n = 158$, $z = 0.030$, $P = 0.976$). However, latency from the onset of courtship until mounting was greater in the dark (median = 230 s, range 38–1857 s) than in the light (median = 74.5 s, range 9–1378 s) ($n = 107$, $z = 5.431$, $P < 0.001$; Fig 1). Similarly, latency from release of the male until mounting was greater in the dark (median = 308 s, range 42–1898 s) than in the light (median = 111 s, range 31–1407 s) ($n = 107$, $z = 5.271$, $P < 0.001$). One potential explanation for this is that females take longer over decisions to accept males when in the dark, needing more time to acquire critical information about their suitors. Alternatively, these differences in mounting latency may simply reflect the relative ease with which males can locate females, orient and mount or with which fe-

males can evade persistent males in the light and in the dark.

The duration of the period during which the male remained mounted on the female in this study was similar to durations reported in previous studies of *S. ocreata* and other *Schizocosa* species (Hebets et al. 1996; Stratton et al. 1996; Norton & Uetz 2005) and was similar in the dark (median = 159 min, range 45–608 min) and in the light (median = 144 min, range 70–719 min) ($n = 107$, $z = 0.372$, $P = 0.710$). In jumping spiders (Salticidae), males may remain mounted for longer when in the dark or in a secluded retreat where they are protected from visually orienting predators (Jackson 1980, 1992; Taylor & Jackson 1999). There are many visually orienting predators in the habitat where spiders were collected for this study, including pompilid wasps, birds, toads (pers. obs.) and conspecifics (Wagner & Wise 1996; Roberts et al. 2003). The similarity of mount duration in the light and in the dark for *S. ocreata* suggests that these spiders lack the apparent risk-dependent copulation tactics of jumping spiders.

ACKNOWLEDGMENTS

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TWO NEW SPECIES OF WOLF SPIDERS IN THE *PARDOSA MODICA* GROUP (ARANEAE, LYCOSIDAE) FROM NORTH AMERICA

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ABSTRACT. Two new species of wolf spiders in the *Pardosa modica* group (Araneae, Lycosidae) are described from North America: *P. knappi* from high-elevation lakeshores in the Sierra National Forest, California, USA, and *P. pedia* from prairie habitats in Saskatchewan, Canada.

Keywords: taxonomy, anatomy, lakeshore, prairie

North American members of the *modica* group of the genus *Pardosa* C.L. Koch 1847 comprise a cluster of more than 20 species of relatively large, dark, hairy spiders. One-half or more of these live among cobble-sized stones on beaches, or among boulders high in the Rocky Mountains. A few, such as *P. glacialis* (Thorell 1872) and *P. algens* (Kulczyński 1908), are high arctic forms. Still others inhabit swamps or bogs at lower elevations or lower latitudes. *Pardosa dromaea* (Thorell 1877) is unusual in habitat, ranging over the Central Plains.

The group has not been revised in total, though Holm (1967, 1970), Kronestedt (1975, 1981, 1988, 1993) and Dondale (1999) have treated most of the included species. Dondale & Redner (1990) and Vogel (2004) defined the group and published reviews, each of which includes a key to species.

Male specimens of the *modica* group can be recognized by the stout, horn-like or tooth-like terminal apophysis and short median apophysis with its beak-like basal process, in the pedipalp. Females possess a flask-shaped epigynal atrium and long, club-shaped spermathecae.

The purpose of this paper is to describe two new species in the group. Body measurements are in mm. Depositories of the type specimens are as follows: AMNH, American Museum of Natural History, New York, New York, USA; CAS, California Academy of Sciences, San Francisco, California, USA; CNC, Canadian National Collection of Insects and Arachnids, Ottawa, Ontario, Canada; DJB, private collection of Donald J. Buckle, Saskatoon, Saskatchewan, Canada; RSM, Royal Saskatchewan Museum, Regina, Saskatchewan, Canada.

SYSTEMATICS

Family Lycosidae Sundevall 1833
Genus *Pardosa* C.L. Koch 1847

Pardosa C.L. Koch 1847:100.
Acroniops Simon 1898:356.
Pardosops Roewer 1955:156.
Chorilycosa Roewer 1960:947.

Type species.—*Pardosa: Lycosa alacris* C.L. Koch 1833, by subsequent designation by the International Commission on Zoological Nomenclature (2003).

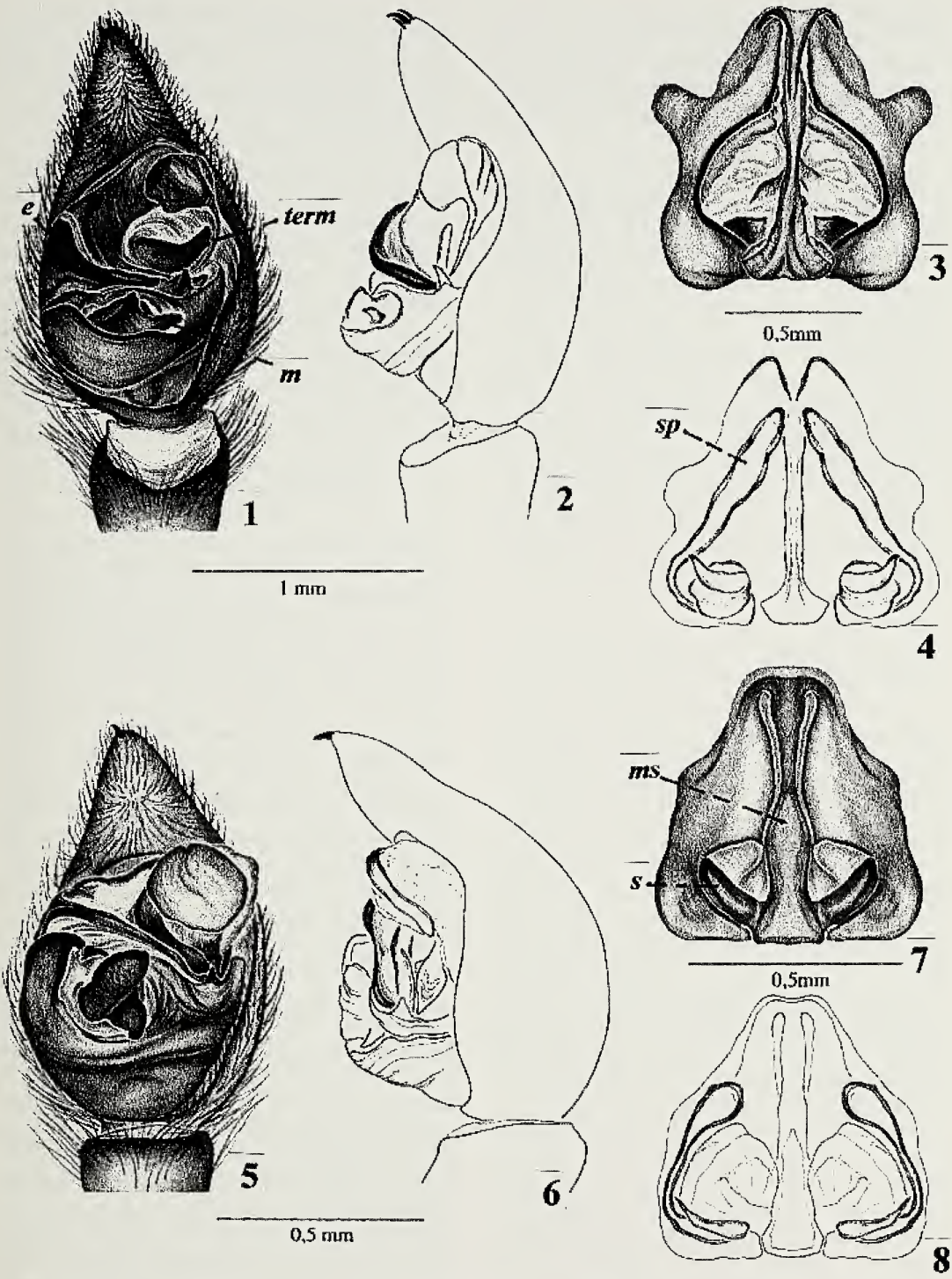
Acroniops: Acroniops heteropthalmus Simon 1898, by monotypy.

Pardosops: Lycosa pontica Thorell 1875, by monotypy.

Chorilycosa: Lycosa arorai Dyal 1935, by monotypy.

Pardosa knappi new species
Figs. 1–4

Type specimens.—UNITED STATES OF AMERICA: *California*: Holotype male, Lower Humphreys Lake (37°15′N, 118°40′W), Sierra National Forest, Fresno County, 3596 m elevation, 30 July 2004, Roland A. Knapp (CAS). Paratypes: 2 females, Wedge Lake (37°16′N, 118°42′W), 3468 m elevation, 15 July 2004, Roland A. Knapp (CAS); 4 males, Mesa Lake (37°16′N, 118°43′W) 17 April 2003, Roland A. Knapp (AMNH); 1 male, Tomahawk Lake (37°15′N, 118°43′W) 3396 m elevation, 22 July 2004, Roland A. Knapp



Figures 1–8.—*Pardosa* spp. 1–4. *P. knappi* new species. 1, 2. Male holotype, pedipalp: 1. Ventral view; 2. Retrolateral view. 3, 4. Female paratype from Wedge Lake, California, USA, epigynum: 3. Ventral view; 4. Dorsal view. 5–8. *P. pedia* new species. 5, 6. Male holotype, pedipalp: 5. Ventral view; 6. Retrolateral view. 7, 8. Female paratype from Grassland National Park, Saskatchewan, Canada, epigynum: 7. Ventral view; 8. Dorsal view. *e,* embolus; *m,* median apophysis; *ms,* median septum; *s,* atrial sclerite; *sp,* spermatheca; *term,* terminal apophysis.

(CNC); 1 female, unnamed lake (37°15′N, 118°41′W) 3590 m elevation, 30 July 2004, Roland A. Knapp (AMNH); 1 female, unnamed lake (37°17′N, 118°42′W), 3547 m elevation, 3 August 2004, Roland A. Knapp (CNC).

Etymology.—The specific epithet is in recognition of the collector of the type series, Dr. Roland A. Knapp, Research Biologist at the Sierra Nevada Aquatic Research Laboratory, University of California at Santa Barbara, California.

Diagnosis.—*Pardosa knappi* males and females key to *P. bucklei* Kronestedt 1975 in Dondale & Redner (1990) and in Vogel (2004). They are distinguished from the latter by the narrower embolus and larger sclerite at the base of the embolus in males (Fig.1), and, in females, by the more slender spermathecae, which have two swellings distally (Fig. 4). Both males and females measure, on average, approximately one-third larger than individuals of *P. bucklei.*

Description.—*Male holotype (Figs. 1, 2):* Carapace brownish black, with short pale median band at dorsal groove, and with pale lateral bands represented by 3 pairs of large spots. Legs basally black, grading to pale reddish brown distally; femur I with 2 dorsal macrosetae, 2 prolaterals (near tip), 0 retrolaterals; tibia I with 2 long dorsal bristles, 2 prolateral macrosetae, 2 retrolaterals, 3 pairs of ventrals; tarsus I with numerous erect setae. Sternum black. Chelicerae reddish black; promargin with 3 teeth, retromargin with 3. Abdomen black dorsally, with dull red heart mark; venter dull black. Pedipalp with stout curved horn-like terminal apophysis, broad straight truncated embolus, and large sclerite at base of embolus; median apophysis with beak-like basal process. Total length 9.63; carapace length 4.73; carapace width 3.74.

Female paratype from Wedge Lake, California, USA. (Figs. 3, 4): Coloration much as in male, but yellow spots on carapace more distinct, and legs showing faint banding. Epigynum with flask-shaped atrium and narrow, essentially straight median septum; septum widening abruptly at anterior and posterior extremities; atrial sclerites distinct, diverging anteriad; spermathecae with two swellings. Total length 10.71; carapace length 4.65; carapace width 3.65.

Variation.—*Males* (n = 5): carapace and legs vary from deep black to dull red, and tarsi from reddish to straw yellow. Total length 9.00–9.63 (mean ± 1 standard deviation: 9.13 ± 0.21); carapace length 4.23–4.96 (4.69 ± 0.26); carapace width 3.24–3.82 (3.54 ± 0.21). *Females* (n = 3): total length 9.71–10.79 (10.25 ± 0.50); carapace length 4.15–5.15 (4.72 ± 0.42); carapace width 3.22–3.90 (3.60 ± 0.29).

Natural history.—All specimens in the type series were collected among rocks on lakeshores in the Sierra National Forest at elevations of 3396–3596 m.

Distribution.—Known only from Humphreys Basin, Sierra National Forest, California, but may be more widespread in other parts of the alpine zone of the Sierra Nevada.

Pardosa pedia new species
Figs. 5–8

Type specimens.—CANADA: *Saskatchewan*: Holotype male, Grasslands National Park (49°10′N, 107°24′W) 11–14 July 1996, A.T. Finnamore (CNC). Paratypes: 3 females, same data as for holotype (CNC); 1 male, same locality, 7–10 July 1996, A.T. Finnamore (DJB); 2 females, same locality, 24–27 July 1996, A. T. Finnamore (CNC); 1 female, same locality, 25–28 July 1996, A. T. Finnamore (DJB); 1 male, 32 km southwest of Beechy (50°43′N, 107°23′W) 3 June 1970, Mike Gollop, from gullet of bird (*Eremophila* sp.) (much damaged) (CNC); 1 male, 10 km south of Cadillac (49°31′N, 107°50′W) 30 May–5 June 1995, J. Pepper (RSM).

Etymology.—The specific epithet is from the Greek word *pedios,* one meaning of which is "dweller of the plains" (Jaeger 1955).

Diagnosis.—This species is not identifiable by the use of published keys owing to the variable number of teeth on the cheliceral retromargin. Males and females most resemble those of *P. furcifera* (Thorell 1875) in size, color, and generalities of the external genitalia. Males differ in the flattened, curved, truncated embolus and much smaller terminal apophysis, and females by the large, distinct atrial sclerites in the epigynum. In both sexes, the lateral bands on the carapace are represented by a series of spots rather than being entire. The habitat also differs: the available specimens of *P. pedia* were found in prairie habitats, whereas those of *P. furcifera* occupy the ground layer of spruce/willow thickets

near the treeline in the boreal forest as well as the arctic tundra itself (Dondale & Redner 1990, map 43).

Description.—*Male holotype (Figs. 5, 6):* Carapace black, with short yellow median band and with lateral bands each represented by a series of yellow spots; front with yellow margin. Legs pale yellow, covered with fine pale pubescence; femora with indistinct dark bands, which are more evident dorsally; femur I with 3 dorsal macrosetae, 2 prolaterals (near tip), 2 retrolaterals; tibia I with 2 dorsal bristles, 2 prolateral macrosetae, 1 retrolateral, 3 pairs of ventrals. Sternum light brown. Chelicerae yellow, darker laterally; promargin with 2 teeth, retromargin with 2. Abdomen black on yellow background, with distinct yellow heart mark; venter pale yellow. Tibia and cymbium of pedipalp dark brown, other segments yellow; tibia covered with erect black setae; cymbium covered with short, semi-erect black setae; terminal apophysis small, tooth-like; embolus long, slender, nearly straight, with tip somewhat flattened and curved; median apophysis with short, broad distal process and short curved basal process. Total length 5.48; carapace length 2.68; carapace width 2.16.

Female paratype from the type locality (Figs. 7, 8): Coloration much as in male holotype, but carapace dark brown rather than black, and leg bands more distinct. Epigynum with median septum long, straight, and narrow, but somewhat widened posteriorly; atrial sclerites large, distinct, pointed; copulatory tubes slender, curved; spermathecae bulbous, with few minute nodules. Total length 6.23; carapace length 2.84; carapace width 2.08.

Variation.—*Males* (n = 2): the sternum may appear dark brown, and tibia I may have dark bands as well as the femur. Total length 5.98, 6.47; carapace length 2.99, 3.49; carapace width 2.18, 2.24. *Females* (n = 5): the slender part of the median septum may extend farther posteriad than shown in Fig. 7. Total length 5.06–6.47 (5.92 ± 0.64); carapace length 2.68–3.49 (3.00 ± 0.17); carapace width 2.08–2.49 (2.25 ± 0.19). In both sexes, the cheliceral retromargins have 2 teeth in some specimens, 3 in others.

ACKNOWLEDGMENTS

Pardosa knappi is respectfully dedicated to Dr. Roland A. Knapp, who collected the type series in the course of his research in the Sierra National Forest. Donald J. Buckle originally recognized *P. pedia* as new to science and submitted the specimens to me for confirmation and description. Nadine Dupérré beautifully illustrated the new species.

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WEB CONSTRUCTION AND MODIFICATION BY *ACHAEARANEA TESSELATA* (ARANEAE, THERIDIIDAE)

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ABSTRACT. The web construction behavior of *Achaearanea tesselata* (Keyserling 1884) was observed in the field and in captivity using suspended wire frames that allowed detailed observations. Construction included three stages: preliminary exploration during which lines were broken, reeled up, and replaced; construction of anchor lines and the upper tangle; and construction and then filling in of the sheet below the tangle. Repeated visits to the mouth of the retreat during tangle construction resulted in the apparent reinforcement of the few lines radiating from this area, a possible adaptation to sense the location of prey in the web, and to facilitate orientation of the spider to prey in the web. Filling in the sheet, which alternated with additions to the tangle, included two previously undescribed behavioral patterns: irregular wandering on the sheet and apparent attachments of the dragline using only the two legs IV to hold previous lines against the spinnerets. The spider needed 1–2 nights, working several hours each night, to make a complete tangle and sheet and added lines and extended both the tangle and the sheet on subsequent nights. Spiders adapted the shapes of their webs to their surroundings.

Keywords: Web construction behavior, web design, aerial sheet web, cobweb spider

The spider family Theridiidae (cobweb or comb-footed spiders), which currently includes 2248 species in 87 genera, is one of the largest and most abundant groups of spiders (Forster et al. 1990; Agnarsson 2004; Platnick 2006). Theridiids construct a variety of webs (Wiehle 1931, 1937; Nielsen 1932; Benjamin & Zschokke 2002, 2003; Agnarsson 2004), most of which are three-dimensional and have often been described as irregular. Recent studies have shown, however, that the patterns of the construction behavior of some non orb-weavers are more regular than the apparent irregularity of their finished webs would suggest (Eberhard 1991; Benjamin & Zschokke 2002, 2003). The construction of non-orb webs is less well studied than orb web construction (Eberhard 1990b).

Species within the genus *Achaearanea*, a relatively derived genus within the family Theridiidae (Agnarsson 2004; Arnedo et al. 2004), spin several types of webs. Apparently the most common are the gumfoot webs (Bristowe 1958; Agnarsson 2004), which are designed to trap walking prey. Gumfoot webs are apparently ancestral in Theridiidae (Benjamin & Zschokke 2003; Agnarsson 2004). The sheet web of *Achaearanea tesselata* (Keyserling 1884), in contrast, consists of a three-dimensional aerial tangle, containing a centrally located retreat for the spider and a tightly woven, more or less horizontal sheet near its lower edge (Eberhard 1972; see Benjamin & Zschokke 2003: fig. 6c). Flying prey that encounter the tangle fall to the sheet where the spider attacks them after having passed rapidly through the sheet itself (Eberhard 1972; Barrantes & Weng 2006). The related species *A.* (= *Theridion*) *japonica* (Bösenberg & Strand 1906) and *A. disparata* Denis 1965 build webs with apparently identical designs (Darchen & Ledoux 1978; Shinkai & Takano 1987). The report of a similar web in *Coleosoma blandum* O. Pickard-Cambridge 1882 by Benjamin & Zschokke (2003) was probably a mistake, due to a mix-up of specimens (Agnarsson pers. com.). The web of *A. tesselata* is mostly composed of non-sticky lines (Eberhard 1972), but there are also a few lines with small, scattered balls of apparently

viscous material (Barrantes pers. com.). There are descriptions of the construction behavior of several types of webs built by theridiids, synotaxids and the closely related linyphiids (Szlep 1965; Lamoral 1968; Eberhard 1976, 1995; Benjamin & Zschokke 2002, 2003, 2004). However, web construction behavior of theridiid aerial sheet webs has never been described. The present study provides a detailed description of the web building behavior of *A. tesselata* and reports modifications carried on the original web design to adapt it to the surroundings.

METHODS

Observations on the web building of *A. tesselata* were made between April and October 2004 in and near San José, Costa Rica. To observe construction behavior, 16 mature females were collected and transported (usually inside their retreats) to the laboratory. Some were kept in a 20 × 30 × 25 cm Perspex® box containing some pieces of wire to provide the spider with points to attach lines; some were placed on a *Yucca* sp. plant (Agavaceae), a species on which webs were commonly found in the field; and some were put on a three-dimensional construction of wire (diameter of wire strand approximately 1 mm) that hung on a nylon fishing line about 1.5 m above the floor. The spiders had difficulty climbing the nylon line and were thus (barring establishment of spanning lines using wind currents) relatively isolated from their surroundings but were nevertheless accessible for close observation. The spiders were fed one *Drosophila* every 1–2 days.

When mature female spiders were collected inside their retreats and the retreat with the spider was then placed on the substrate, the spider often began to suspend the retreat within one to two minutes independent of the time of day. All other behavioral observations were made between 19:00 and 24:00 h. Some night observations were made using a dim light that illuminated objects behind the web, thus making the silhouette of the spider visible. The spider was occasionally illuminated directly for a few seconds with a flashlight or a red laser pointer for more detailed observations. Other observations were made using the infrared "night shot" option of a SONY TRV 80 digital video camera. Both tangle and sheet construction behavior were taped (a total of 25 min). We observed at least parts of the construction of 20 webs in captivity and five webs in the field. Construction of webs in the field was induced by destroying part or most of the previous web. By turning on a light at night in the room with the spider, it was possible to inhibit web construction thus allowing us to lengthen or shorten the amount of time the spider had on a given night to work on its web. We did not attempt to measure durations of behaviors.

We measured 15 webs of mature females in the field, another 10 webs of mature females in captivity, and three webs of juveniles in captivity. We measured the "maximum length" of the sheet (not counting anchor lines extending beyond the sheet), and the "maximum width" perpendicular to this dimension. The height of the web was recorded from the sheet to the upper edge of the tangle. The variance of the ratio between maximum length and the maximum width in webs in the field and in captivity were compared with the Levene-Test (SPSS). Data were also checked for homogeneity of variances (t-Test, SPSS).

A voucher specimen of this study was deposited in the Museo de Zoología of the Escuela de Biología of the Universidad de Costa Rica.

RESULTS

Web construction.—With the exception of lines laid to suspend the retreat, the entire web building process took place at night.

Preliminary suspension of the retreat: Mature female spiders collected inside their retreats usually started suspending the retreat shortly after being placed on the new substrate. After attaching the dragline to the retreat by touching her spinnerets against its surface and while holding the dragline with one outstretched leg IV, the spider climbed upward and attached the dragline to a strand of wire. She then walked back under the newly laid line and attached it again to the retreat, thus doubling the line. Then she returned to the wire strand and climbed a little higher and attached again, repeating this several times. By repeating this process and connecting the new lines with each other, the retreat was pulled into a hanging position a few cm above the substrate. Usually the spider stayed on one side of the cage, but in two cases she climbed up the opposite side and attached the dragline.

The spider then entered the retreat and did not resume construction until night.

Spiders with egg sacs or juveniles in their retreats (n = 8) did not abandon their retreats, and suspended them as just described. In contrast, each of the five adult females without egg sacs abandoned their retreats as soon as they were released (P = 0.0008, Fisher Exact Test). Three of them left the retreat and hid motionless under a piece of leaf or wire and waited there immobile until night. The other two climbed up a wire strand and constructed a few lines and hung immobile under these lines until night.

Preliminary exploration: Undisturbed spiders started web construction around 19:00 h, about 1 h after sunset. The adults without egg sacs explored the surroundings and those not in a cage moved up to 3 m before making a web. During the exploration stage, the spider sometimes broke the line on which she was walking, reeling it up and replacing it with her dragline as she moved. The spider also repeatedly attached her dragline to a plant leaf or wire strand and then dropped slowly 20–30 cm. If she reached an object below, she attached her dragline. Otherwise she climbed back up her dragline, packing it into a small white mass (Fig. 1), which she left attached to the line from which she had descended.

Figure 1.—Mass of loose silk seen under the compound microscope.

Construction of the anchor lines and the tangle: The first lines often extended up to 30 cm, and the web soon became three-dimensional. We could not discern a pattern in the lines laid at this stage. Both direct observations and video recordings showed that when attaching the dragline to another line, the spider held the dragline with one leg IV and grasped the other line with ipsilateral legs III and IV, bringing this line toward the spinnerets and at the same time moving her abdomen ventrally toward the line (Fig. 2). The spider walked underneath silk lines at all times, and held her dragline with the tarsus of one leg IV. Periodically she switched the leg IV that held the dragline.

Constructing an anchor line to the substrate or wire strand during tangle construction, the spider attached her dragline to the retreat or another web line and then moved to the end of a line attached to the substrate/wire strand, then moved further along the substrate/wire strand before attaching her dragline; she then returned along the newly laid line, doubling it with her dragline. In attaching to a strand of wire, the spider often moved to the side of the wire away from the web before attaching; the new line was thus partially curled around the wire. Anchor lines and associated lines in a partially complete web included multiple lines that were more or less parallel and converged on the anchor (Fig. 7). The attachments of anchor lines in finished webs were heavily reinforced, consisting of multiple lines attached at slightly different points to the substrate/wire strand.

The spider repeatedly interrupted tangle construction to return to the mouth of her retreat, then left again to lay further lines. One spider returned to the mouth of her retreat an estimated 20–50 times during about 90 min of tangle construction. Despite these many trips to the mouth of the retreat, only a few lines connected the mouth with the tangle in a finished web (Figs. 11, 12). This probably re-

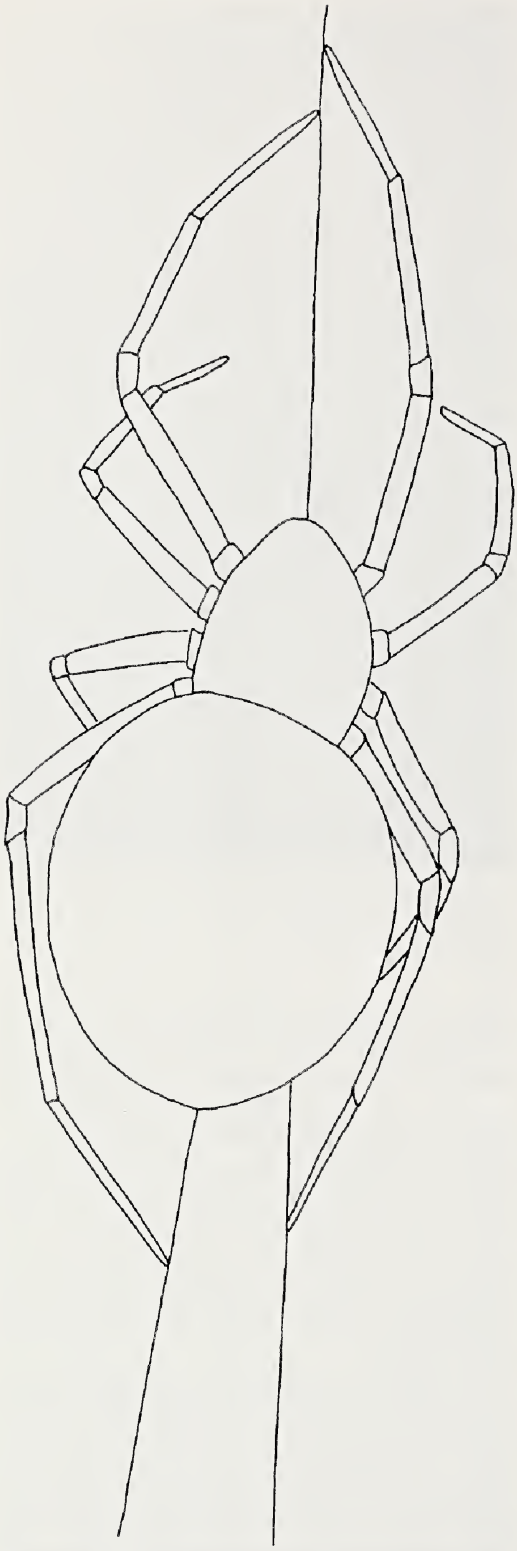
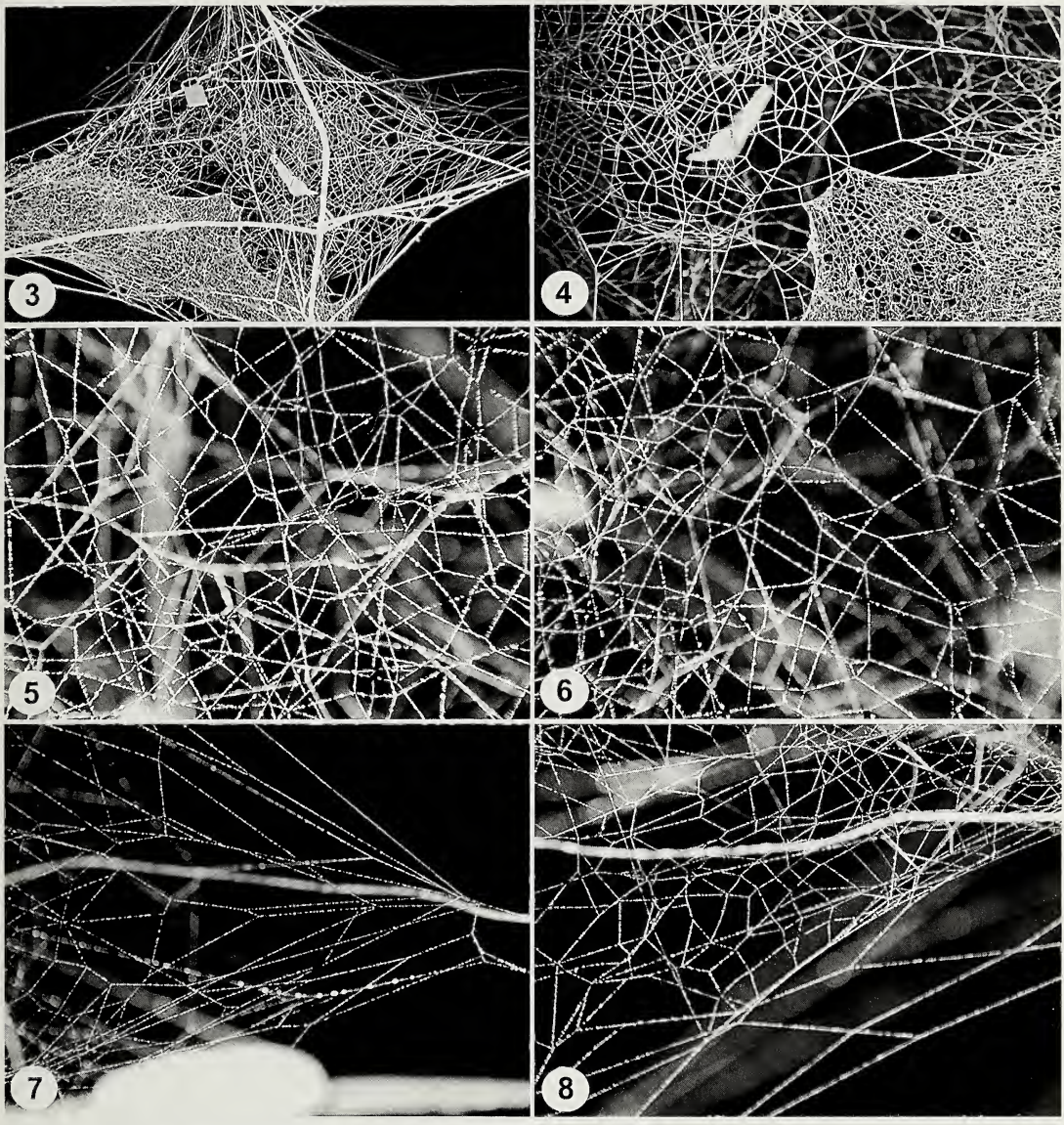


Figure 2.—Diagrammatic representation of the position of a spider attaching her dragline to another line.

sulted from the fact that the spider, when she returned to the retreat, consistently attached her dragline to the tangle 1–2 cm from the retreat, then moved directly to the retreat along a pre-existing line and attached her dragline again at the mouth of the retreat. When leaving to build more tangle, she reversed this process, attaching the dragline to the retreat mouth and then again only 1–2 cm from the retreat before moving away to resume tangle construction. Presumably these short lines laid near the retreat were generally laid along lines that were already in place; this would explain why there were few lines present in finished webs, despite the many visits to the retreat.

The spider made further descents during tangle construction. When she did not encounter substrate below, she climbed back up and moved on; leaving the white mass of packed up dragline silk attached to the tangle. The spider also sometimes broke lines in the tangle but simply released them and allowed them to sag loosely rather than reeling them up. One possible pattern in tangle construction was that more lines were laid above than below it during earlier stages, while more were laid below it later, but further observations will be needed to confirm this.

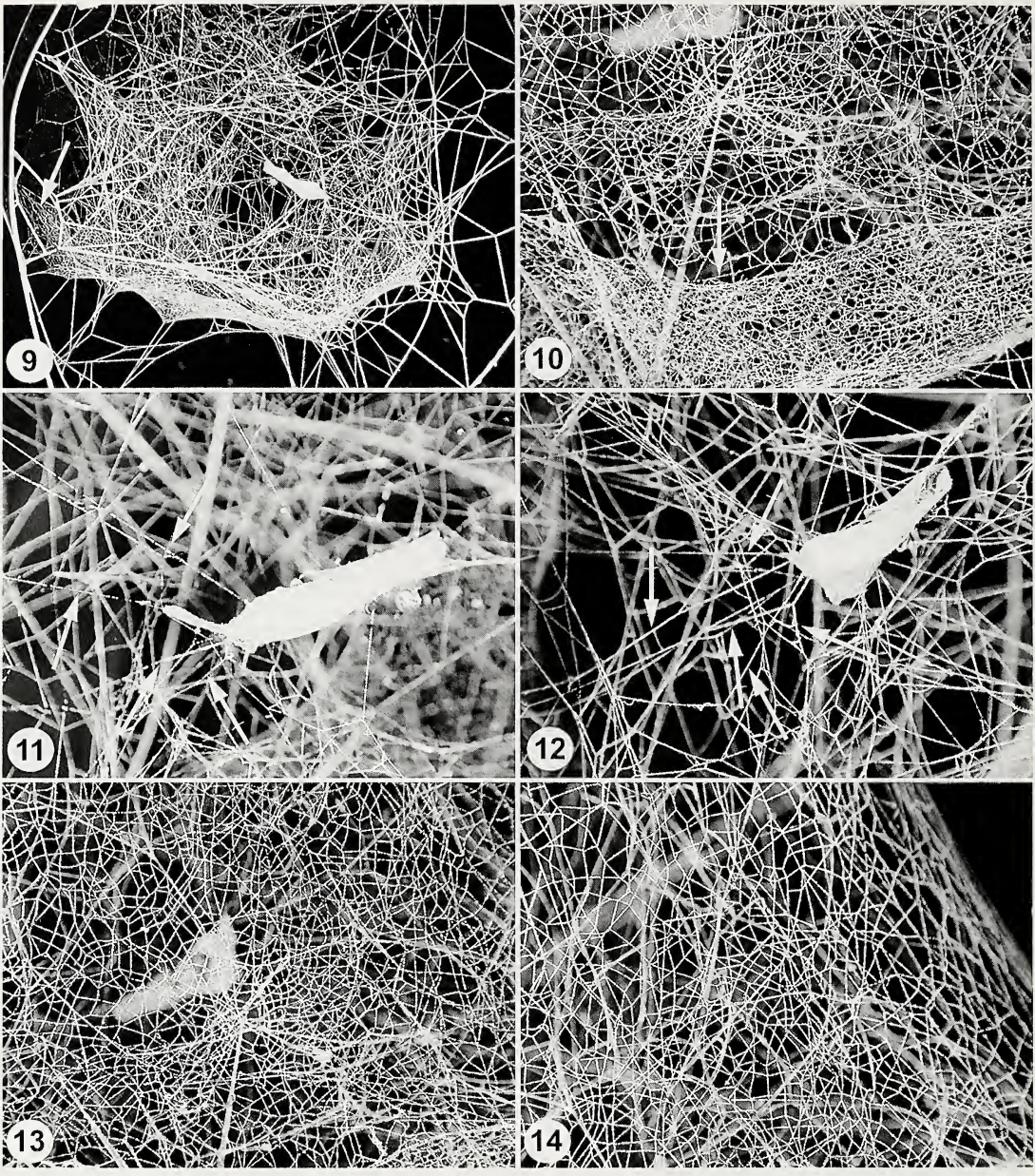
Construction of the sheet and filling in the sheet and tangle: The sheet was not built until an extensive tangle had been spun. When the spider was disturbed frequently during tangle construction by attempts to observe her with a light (n = 7 in captivity), no recognizable sheet was produced until the second night. Spiders allowed to build without serious disturbance produced both tangle and a sheet on the first night and then added more lines to both on the second night, so that they both became appreciably more dense (n = 12 in captivity, n = 5 in the field). Further construction was seen on the third night (n = 8 in captivity) and in two cases further extension and filling in also occurred on the fourth and fifth nights. During the later stages of filling in the sheet, the spider spent periods of up to 5 min walking under the sheet, apparently attaching her dragline to the sheet approximately 3–5 times each cm she moved (we could not see individual lines and presumed that attachments were made on the basis of the spider's behavior). Filling in the sheet and the tangle were not two discrete stages, but alter-



Figures 3–8.—Photographs of a partially complete repair of a web in which approximately half of the sheet was destroyed and the spider was allowed only about half the following night to repair it. 3. Ventral view of the sheet, showing a portion that was more than one week old (lower left) and the repaired portion built the preceding night (the thick lines are wire frame in which the spider built the web, and the object in the middle is the curled leaf retreat; the frame hung from a chain that is visible above the web); 4. Close-up of ventral view of the border between old and new sections of the sheet; 5, 6. Close-up views of the new area of the sheet, showing the substantial numbers of approximately parallel lines; 7. Close-up ventral view of an edge of the sheet where many more or less parallel lines converge on an anchor line; 8. Ventral view of an edge of the sheet where an apparent sharp turn-back by the spider is evident (arrow).

nated with one another. After a period of sheet construction, the spider usually climbed through the sheet and 1–2 cm up into the tangle, producing a line connecting the sheet to the tangle above, then either moved to a different region of the sheet or to the mouth of the retreat. In later stages of construction the spider appeared to dedicate longer periods of time to sheet construction ($n = 4$).

Apparently the general framework for the



Figures 9–14.—Photographs of a more completely repaired sheet, in which the spider was allowed the entire night to repair partial damage to a sheet older than a week. 9. Lateral view of web with sheet, and tangle and curled leaf retreat above the sheet. The arrow marks the upward lip at the edge of the sheet; 10. Ventral view of the border between previous sheet (below) and newly built repaired sector (above); 11–12. lines radiating from the mouth of the curled leaf retreat (arrows) in a tangle that was more than 1 wk old (sheet below the retreat was removed); 13–14. Ventral views of repaired sheet, showing diversity of tangle size and lack of consistently parallel lines in central portion of sheet (13) and near the edge where sheet turned upward (14).

sheet was laid out first, and then gradually filled in (Fig. 3). We were not able to distinguish, however, the first stages of sheet construction; it is possible that this was because we did not observe spiders at the right stage of construction. We were not able to discern a pattern in the path the spider followed as she filled in the sheet, other than that she

sometimes seemed to spend time in only one part of the sheet, and then changed to work in another part of the sheet (Fig. 15). Photographs of one incomplete web suggested that the spider began to fill in the sheet in a more central area with a relatively sparse but evenly spaced array of lines (Figs. 3, 4) and then later included more peripheral areas and increased the density of lines (Figs. 13, 14). The sheet was not gradually extended in an orderly manner from a central point (as, for example, in the sheet-weaving theridiid, *Chrosiothes* sp. Eberhard, pers. obs.), nor did the spider move regularly from one edge of the sheet to another. Many of the relatively evenly dispersed lines in an early stage sheet were approximately parallel to each other (Figs. 5, 6), perhaps because of the pattern illustrated in Fig. 7. Further filling in of the sheet resulted in lines with a greater variety of orientations. Further observations are needed to check whether the patterns in Figs. 3–8 and 9–14 also occur in other webs.

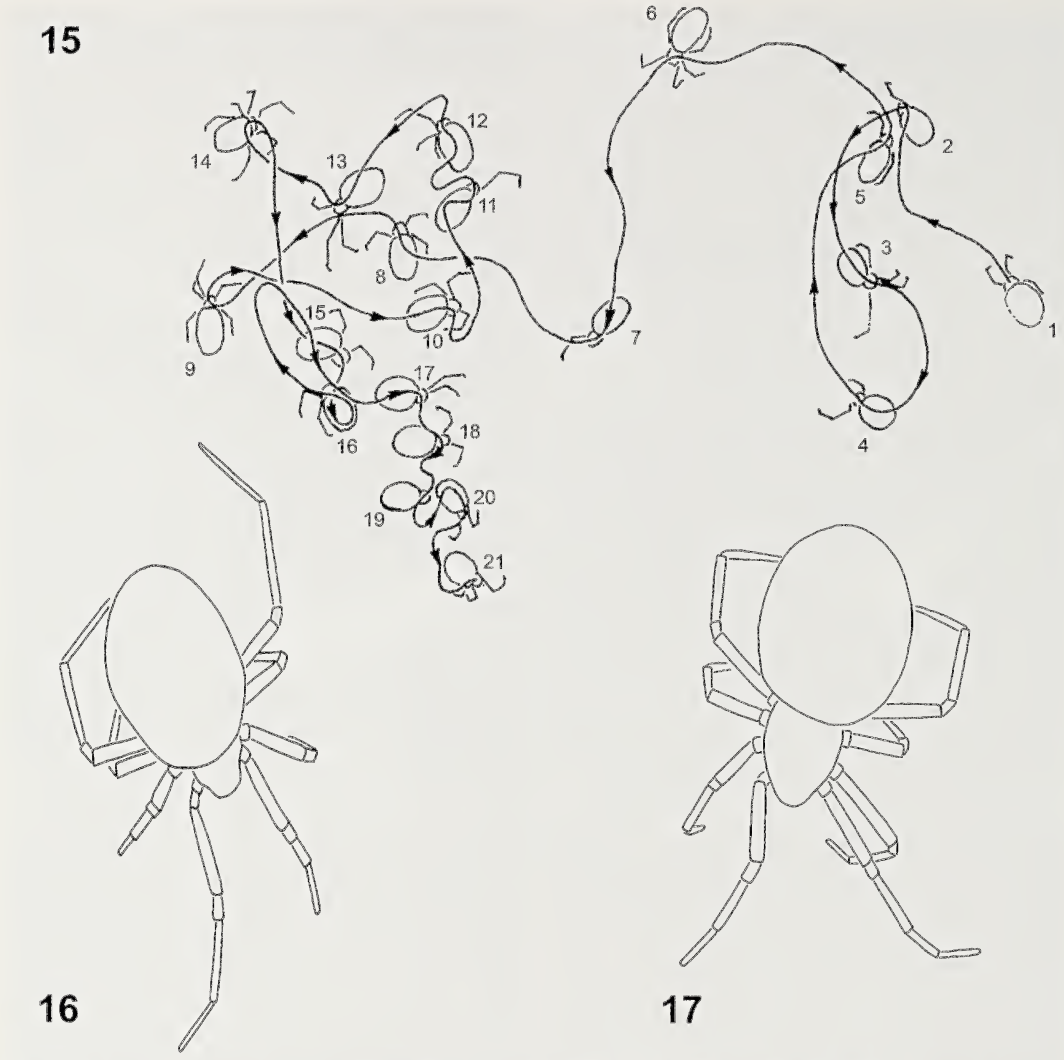
Early in the construction of one sheet the spider made 180° turns repeatedly (Fig. 8), while later such turns were very rare as she wandered. At least in the later stages of filling in the sheet, this spider and others moved more rapidly in an irregular pattern, walking forward, sideways, and sometimes turning erratically in partial or complete circles (Fig. 15). While moving more or less laterally, the spider's lead leg I was often extended anteriorly and laterally and tapped actively. As she moved, the spider appeared to attach her dragline rapidly and repeatedly to the sheet (we could not see individual lines, however, and presumed that attachments were made because of the spider's behavior). Frame by frame analyses of video records revealed that as she appeared to attach her dragline, the spider sometimes held one leg IV behind her abdomen (presumably holding the dragline as during tangle construction), while the other leg IV and her ipsilateral leg III apparently held a line in the sheet; her spinnerets were pressed against the sheet between the tarsi III and IV when she tilted her abdomen laterally and ventrally (Fig. 16). In other presumed attachments made later during the construction of the same sheet, however, the spider's two legs IV apparently briefly grasped the sheet simultaneously on either side of her spinnerets and apparently pulled the sheet (or at least held it) while her abdomen was flexed ventrally and the spinnerets apparently touched the sheet and attached her dragline (Fig. 17). The spider then moved onward with neither leg IV appearing to hold her dragline.

Although this second mechanism of bringing the spinnerets into contact with the sheet would seem imprecise in positioning the spider's spinnerets on a single line in the sheet, in a sample of 75 attachments on a finished sheet examined under a compound microscope, 66 were to a single line. Attachments were relatively dense. In one sheet that was more than a week old, there was an attachment disk in 77 of the 188 cases in which one line crossed another.

While filling in the sheet and the tangle during the first or subsequent nights, the spider also sometimes added new anchor lines from the tangle or from the sheet to the substrate/wire strands. Some additions resulted in extension of both the tangle and the sheet, including additions to the sheet with an upward tilt (arrow in Fig. 9). Web extensions were noted in seven cases. On one occasion the spider also adjusted the position of her retreat by pulling it a few mm higher and toward the middle of the web.

During all stages of construction the spider paused frequently to clean her legs. She stopped construction and passed the tips of her legs, one by one, through her mouth region. Legs IV were passed over the sides of her abdomen before being brought to her mouth.

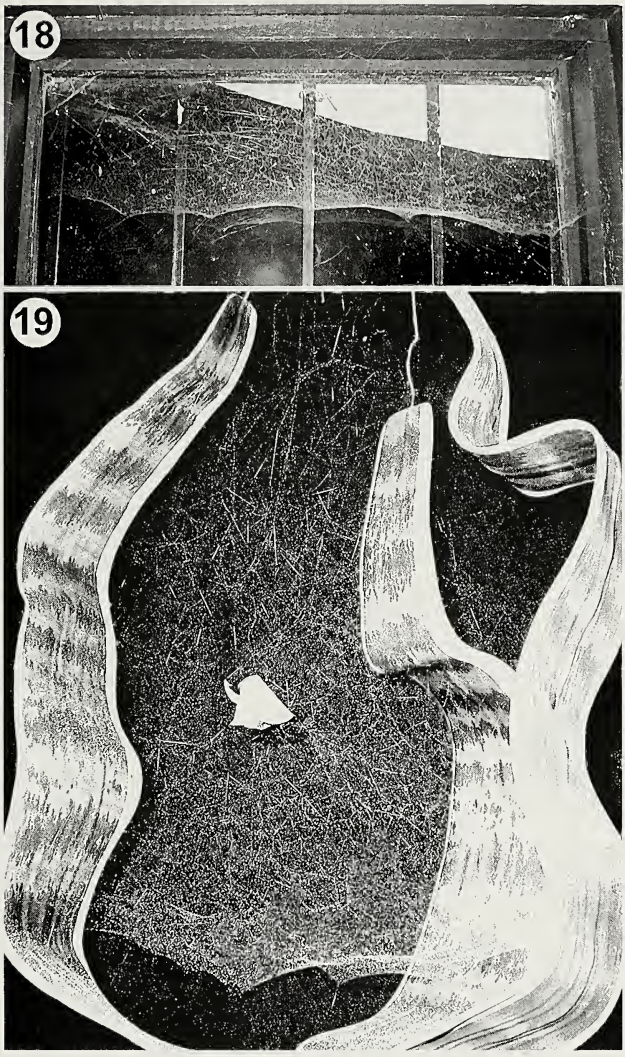
General description of the web and variations.—The webs of adult females in the field were commonly attached to three to five relatively large, stiff leaves (e.g., *Agave* sp. plants) or to rigid branches. All webs in the field included a three-dimensional tangle with a dense horizontal sheet near its lower edge. The edges of the sheet often slanted upward approximately 1 cm (Fig. 9). The webs of the smallest juveniles with webs of their own (at least the first two instars are spent in the mother's retreat) had designs that were not distinguishable from those of adult females. Most webs (16 of 20) had a detritus retreat more or less in the center of the tangle, approximately five to ten cm above the sheet. Retreats were made of dry leaves (often curled) or other plant material. The spider rested upside down at the mouth of its retreat during the day. Spi-



Figures 15–17.—Behavioral patterns during construction. 15. Path of a spider during 100 s of filling in the sheet as it wandered. The spider's position and orientation is shown every 5 s. When the direction of the path and the orientation of the spider's body are not the same, she was moving laterally rather than straight forward; 16, 17. Positions of spider during sheet filling-in behavior when she was apparently attaching her dragline to the sheet by holding a previous sheet line to her spinnerets with her ipsilateral legs III and IV (16) or with her two legs IV (17). (All traced from video images.)

ders without a detritus retreat rested at about the same position in the tangle.

The mean values (± SE) of web dimensions of adult females describe a more or less oval sheet, with a maximum length of 23.8 ± 8.9 cm and maximum width of 16.3 ± 4.5 cm; the mean height was 16.3 ± 3.5 cm. The height of the 15 webs in the field and the 10 in captivity ranged between 11.2–25.1 cm, while the maximum length and the maximum width measurements varied more (6.0–49.0 cm). The mean ratio of the two diameters did not differ significantly between field and captivity ($P > 0.05$, Levene-Test), but there was significantly greater variance in this ratio in webs built in captivity ($P < 0.05$). This was probably due to adjustment of web forms in captivity to unusual surroundings. The most striking examples of this were two webs with elongate and nearly rectangular sheets that were built in window frames. The most extreme web measured 49.0 cm in maximum



Figures 18, 19.—Web modification: 18. Elongated web built on a window frame; 19. More symmetrical web built subsequently by the same spider on a plant.

length and only 6.0 cm in the maximum width (Fig. 18). When this spider was then placed in a three-dimensional wire frame she built a much more typical web with a more or less oval 23.3 × 16.1 cm sheet (Fig. 19).

DISCUSSION

The absence of break and reel (or "cut and reel") behavior during tangle and sheet construction in *A. tesselata* must be considered a design feature of their web construction behavior rather than an omission due to an inability to break and reel because *A. tesselata* broke and reeled lines with typical dexterity during exploration. Break and reel behavior occurs during the construction of orb webs (Eberhard 1982, 1990a; Coddington 1986; Griswold et al. 1998), and is also performed by some other theridiids such as *Chrosiothes tonala* (Levi 1954) (see Eberhard 1991), *Phoroncidia studo* Levi 1964 (see Eberhard 1981), and *Argyrodes* sp. (Eberhard pers. obs.). Benjamin and Zschokke (2002, 2003) reported that they did not see break and reel behavior in *A. tepidariorum* (C.L. Koch 1841) or *Steatoda triangulosa* (Walckenaer 1802). It is not clear if it also occurs in these species very early during web construction as in *A. tesselata* (only late in this study did we observe its occurrence). Breaking and reeling a line allows the spider to move points of attach-

ment and to adjust the tensions on newly laid lines; when a spider does not break and reel a line, in contrast, the line is reinforced. Perhaps web strength is more important than attachment or tension adjustments for *A. tesselata*.

Achaearanea tesselata also broke lines during tangle construction, but then released them to sag in the web, as also occurs in *S. triangulosa*, which cuts and bundles up old or loose lines (Benjamin & Zschokke 2002). These observations and observations of attack behavior (Barrantes & Weng 2006), also show that *A. tesselata* is able to cut lines rapidly and surely. The failure of *A. tesselata* to bundle up and remove these loose lines could be due to an inability to eat and recycle silk. Alternatively, perhaps the loose lines make the web a more effective trap, as with the "screw lines" of *Pholcus phalangioides* (Fuesslin 1775) (see Kirchner 1986).

Although *A. tesselata* was able to construct a functional finished web within 1–2 nights, webs in the field remained in place for up to several weeks during which time they were repaired and extended. Holes in the sheet resulting from prey capture were repaired the next night. Gradual accumulation of lines over periods of several days also occurs in several other theridiids (Szlep 1965; Lamoral 1968; Benjamin & Zschokke 2002, 2003; Barrantes pers. obs. on *Chrysso* sp.). In contrast, *Steatoda lepida* (O. Pickard-Cambridge 1879), *Latrodectus mactans* (Fabricius 1775) (Lamoral 1968; but see Szlep 1965 on *Latrodectus* spp.), and *Synotaxus* spp. (Eberhard 1976, 1995) in the related family Synotaxidae (Agnarsson 2003) are reported to build a new web each night starting at nightfall.

Web construction by *A. tesselata* can be roughly divided into three stages: exploration, construction of the anchor lines and the tangle, and construction of the sheet and then filling in both tangle and sheet. However, these stages were not easily distinguishable, especially early in construction and sheet filling was frequently interrupted by additions to the tangle. Photographs of partially completed webs suggested further possible divisions in sheet construction behavior, including a very early stage of filling in that was concentrated in the central portion and a later addition to the sheet of upward sloping outer margins (Fig. 10). These preliminary suggestions require further confirmation.

Several details of construction by *A. tesselata* resembled those in other species of theridiids, as in *S. triangulosa*, *A. tepidariorum*, and *Theridion* spp (Benjamin & Zschokke 2002, 2003). *Achaearanea tesselata* built only at night, held its dragline with one leg IV during tangle construction, doubled new lines it attached to the substrate, used existing thread lines as scaffolding to expand the web, and did not break and reel lines during tangle and sheet construction. In addition, females of *A. tesselata* with egg sacs or juveniles in their retreats began construction by making anchor lines that connected the retreat to the substrate, as in *S. lepida*, *S. triangulosa*, and *Latrodectus* (see Szlep 1965; Lamoral 1968; Benjamin & Zschokke 2002). A further resemblance to *L. tredecimgutattus* (Rossi 1790) (see Szlep 1965) was that the upper portion of its nonsticky web (the tangle) was built before the lower portion (the sheet).

Several more general patterns of *A. tesselata* behavior also resembled those of other theridiids. Construction of tangle lines prior to building the sheet, repeated returns to the retreat during tangle construction, alternation between sheet and tangle construction, and additions to both tangle and sheet on subsequent nights all resemble similar overall ordering, alternation of activities, and gradual extension of tangle and gumfoot lines in *Latrodectus* spp., *S. triangulosa*, and *A. tepidariorum* (Szlep 1965; Benjamin & Zschokke 2002, 2003). The general patterns of an approximate but not strict ordering of behavioral patterns, and of gradual extension and filling in of the web over several nights are probably very ancient, as they are present in such distant relatives as austrochilines (Lopardo et al. 2003). If theridiids are derived from orb weavers (Coddington 1986; Griswald et al. 1998), whose construction behavior is much more rigidly ordered and in which gradual web extension does not occur, then these less ordered aspects of construction must be convergently derived in theridiids.

The behavior of *A. tesselata* as the spider approached and left the mouth of the retreat (attach dragline 1–2 cm away, walk directly to retreat and attach, then attach again only 1–2 cm from the retreat while leaving) was presumably responsible for the low number of short lines radiating from the retreat mouth in finished webs (Figs. 11, 12). This design may

explain the surprising ability of *A. tesselata* in retreats to orient their attacks in the direction of prey trapped in the web even before leaving the retreat (Barrantes & Weng 2006).

The relatively short exploration stage we observed is similar to that of *Steatoda triangulosa* (see Benjamin & Zschokke 2002) and of several other theridiids (Szlep 1965; Lamoral 1968). Exploration by *A. tesselata* in the field is undoubtedly sometimes much longer, however, as spiders presumably must search for rigid objects that they use to support their webs. The descents during exploration and web construction, which also occur in *L. tredecimguttatus* (see Szlep 1965) and *S. triangulosa* (see Benjamin & Zschokke 2002), probably inform the spiders of the presence of objects below to which they can attach or that they need to avoid (Szlep 1965; Benjamin & Zschokke 2002). The relatively short duration of exploration in captivity may be an artifact of the structural simplicity of the observation area in captivity (Benjamin & Zschokke 2002). However, one of our observation settings, a plant in the family Agavaceae, offered a similar complexity to that of natural sites, and exploration was not noticeably longer.

The homology of the sheet in *A. tesselata* to structures in the webs of other theridiids is not clear. All current evidence shows that the ancestral web design for theridiids is the gumfoot web (Benjamin & Zschokke 2003; Agnarsson 2004). Other species of *Achaearanea* make various types of webs, including gumfoot webs, and many have very sticky lines, not sheets (Benjamin & Zschokke 2003; Agnarsson 2004). The lower web layer of the gumfoot web of *L. tredecimguttata* (see Szlep 1965) is structurally somewhat similar to *A. tesselata* sheets. Construction behavior is somewhat different, however, in *L. tredecimguttata*: the spider fills in this layer in a regular back and forth pattern of movements from retreat to periphery, rather than by wandering. The erratic wandering and the attachment of the drag line to lines held by both legs IV during sheet construction by *A. tesselata* (Fig. 15) have not, to our knowledge, been reported for any other theridiid species or, for that matter, for any other spider. Their functional significance is not clear.

Attachment of anchor lines by *A. tesselata* to the far side of objects such as wires probably makes the attachments more secure. This can be appreciated by comparing an attempt to free a piece of adhesive tape stuck to a surface by pulling on it parallel to the surface, as compared with pulling on it perpendicular to the surface. Such "around the corner" attachments have apparently not been reported in theridiids, but similar attachments are made by araneoid orb weavers such as *Nephila clavipes* (Linnaeus 1767), *Leucauge marinana* (Taczanowski 1881), and *Plesiometa argyra* E.O. Pickard-Cambridge 1899, and also by the more distantly related *Philoponella vicina* (O. Pickard-Cambridge 1899) (Uloboridae) and *Diguetia albolineata* (O. Pickard-Cambridge 1895) (Diguetidae) (Eberhard 1990a, 2001, pers. obs.). Some previous studies of theridiid web construction behavior were made in smooth-walled containers where this kind of attachment is not feasible; this may account for this behavior not having been noted before.

Achaearanea tesselata of all ages always made the same basic web design with an extensive tangle above a dense, horizontal sheet. Under normal conditions the sheet was relatively round, but spiders modified the form of the sheet radically to adapt it to unusual conditions. The greatest modification of the form (to an approximate rectangle of 49 × 6 cm) resulted when a spider deserted a less restrictive building site to choose this unusual site on its own. Flexibility in web shape may be common in theridiids. The general design of different webs of the theridiids *Steatoda* (= *Teutana*) *castanea* (Clerck 1757) and *Latrodectus* spp. remained the same, but the shapes of their webs were influenced by the spaces in which they are built (Wiehle 1931; Szlep 1965). Benjamin & Zschokke (2003) also mention "variable behaviors to build successive webs," although they do not specify species or behaviors.

This study is preliminary in many respects. Further observations on the first stages of sheet construction, the site of the first filling in of the sheet, the apparent attaching movements during sheet construction, as well as the significance of the frequent returns to the retreat during tangle construction and the possibility that different lines are laid under systematically different tensions (Lamoral 1968) are all needed.

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REGENERATIONAL LEG ASYMMETRY IN DAMAGED *TROGULUS NEPAEFORMIS* (SCOPOLI 1763) (OPILIONES, TROGULIDAE)

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ABSTRACT. Among the trogulid harvestman *Trogulus nepaeformis* (Scopoli 1763) collected from sixty localities in Slovenia and northeastern Italy we found many individuals with evidence of old leg injuries. In a few localities, injured individuals accounted for 30% of the total. In non-autotomizing trogulids, in vivo damage to leg articles is characterized by rounded regeneration of the stumps with pseudonormal terminal chaetotaxy, in some cases including a secondary claw. This damage, probably caused by shrews, was considered appropriate for analysis of the regenerational asymmetry, or RA, of legs. In 169 available regenerated specimens, the lengths of preserved articles on the damaged legs were compared to those on the undamaged ones. In the damaged specimens, the range of leg article RA was significantly larger in comparison to undamaged specimens. This is considered to be a direct consequence of the regenerative processes in the leg stumps. The damage was most frequent in 2nd leg, followed by 1st, 3rd and 4th, indicating that such wounds were not stochastic, and probably appeared during the forward motion of the troguli. The stomach contents of 204 shrews were examined and the remains of *T. nepaeformis* were found in two individuals demonstrating for the first time that shrews do feed on this species.

Keywords: Leg damage, regeneration, regenerational asymmetry, predation, shrews

The genus *Trogulus* is known as taxonomically the most difficult of the European harvestmen (Martens 1988), but is of particular interest because trogulids do not autotomize legs and individuals with damaged and healed legs can be found. Shrews and hedgehogs have been reported to prey on harvestmen although the harvestmen species have rarely been mentioned (Yalden 1976; Churchfield et al. 1991; Mitov 1995a; Haberl 2002). Prior to this study, troguli have not been explicitly reported to have leg stumps nor to be preyed upon by insectivores.

Matching asymmetry is defined as the asymmetry of two separate structures, one on each side of the body, existing as mirror images of each other (Mardia et al. 2000; Klingenberg et al. 2002). Fluctuating asymmetry (FA) relies on small differences between corresponding left and right body parts, R-L. The R-L items are normally distributed about the mean, which is not significantly different from the zero value. FA has often been used in detecting stresses and indicating the individual condition of organisms (Palmer & Strobeck 1986; Klingenberg et al. 2002). In cases of directional asymmetry (DA), the R-L is normally distributed about the mean, but the mean departs significantly from zero, while in antisymmetry, AS, the R-L is more or less bimodally distributed (Palmer & Strobeck 1992). Regenerational asymmetry (RA) arises most likely from a single event during ontogeny (Uetz et al. 1996), and in stochastical injuries, the R-L are expected to be distributed in the same way as FA.

The absence of leg autotomy in troguli presented the opportunity to study the impact of damage on the leg asymmetry within the opilionid *T. nepaeformis*. Most of the in vivo injuries in *T. nepaeformis* appeared to be caused by insectivores and were most frequent in the most exposed second legs. Our goals were to analyze the impact of in vivo leg dam-

age on the RA of their limbs, and to check whether shrews are causing this damage in troguli.

METHODS

The RA analysis dealt with 169 damaged *T. nepaeformis* (71 males, 98 females) from 29 localities in western Slovenia and northeastern Italy (range 13°10′–14°50′E, 45°30′–46°50′N). Most of the damaged specimens were collected in Korte (13°39′38″E, 45°29′20″N), Idrija (14°1′59″E, 46°0′13″N) and Tarcento (13°16′01″E, 46°11′54″N). From these localities we also collected undamaged specimens (39 males, 57 females). We analyzed only those damaged individuals that had a single regenerated leg with the opposite leg undamaged. Freshly injured individuals, those missing entire articles, and four with abnormally elongated secondary end-articles were not included.

We measured legs by laying them out on a slide in a lateral position and covering them with a second slide. If necessary, the upper slide was additionally loaded to press the leg in this position. Leg scanning was done under a Nikon SMZ-2T binocular microscope using a Eurocam (Euromex, Netherlands) digital camera connected to a personal computer. The lengths of the articles (Fig. 1) were measured using the TPS Dig program (Rohlf 2001). In testing RA, 19 of 30 leg articles with at least three items each were analyzed.

Two hundred and four soricids from six localities in the same area in Slovenia were investigated for their stomach contents by heating the stomach contents in 10% KOH and examining chitinous remains under a microscope.

Statistical analyses were carried out separately in the damaged and undamaged adult individuals, and in both sexes. Repeatability measurements were carried out on 14 characters of 67 randomly chosen damaged individuals. A mixed-model ANOVA was used for estimating asymmetry relative to measurement error (individual interaction X side), using Palmer's (1994) approach. The directional asymmetry (DA) was tested with a one-sample t-test, antisymmetry (AS) by using measures of platykurtism, and departures from normality with a one-sample Kolmogorov-Smirnov test. One outlier, exhibiting extreme

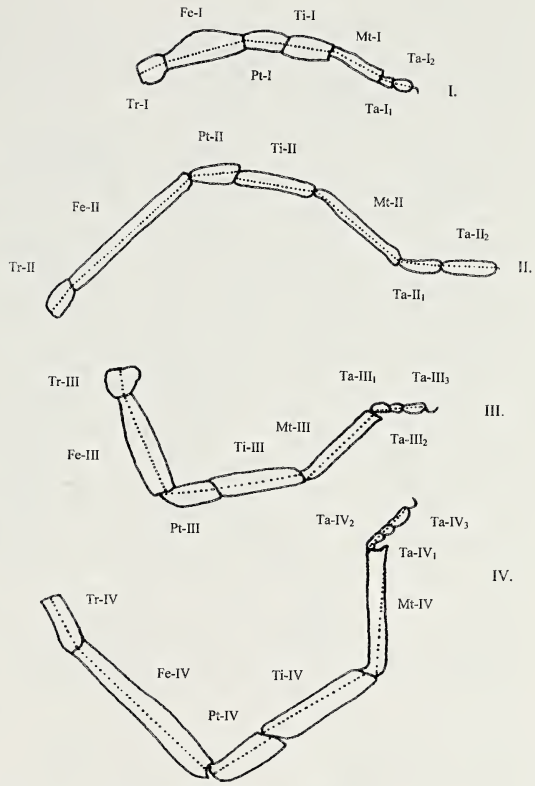

Figure 1.—Standardized measurements (dotted lines) of the leg articles in *T. nepaeformis*. I–IV = legs, Tr = trochanter, Fe = femur, Pt = patella, Ti = tibia, Mt = metatarsus, Ta = tarsus.

departure from normality was excluded from further analyses.

The RA measure was provided using the formula FA4 for the measure of FA according to Palmer (1994): RA = var (R–L), where "var" is the variance, and "R" and "L" are the right and the left item, respectively (Palmer & Strobeck 1986). The differences between sexes, and between damaged and undamaged individuals were tested using One Way ANOVA, the *F*-test for testing differences between means, and Levene's test for homogeneity of variances.

The centroid within the prosoma, based on the equal radial distance of the tips of both the longest, the 2nd and the 4th legs, nearly coincides with that based on the equidistance of the distal parts of the coxae, and was called the leg centroid. It was used in testing frequencies of damaged articles for their stochasticity. The body centroid is not appropriate for this purpose because in this way, the

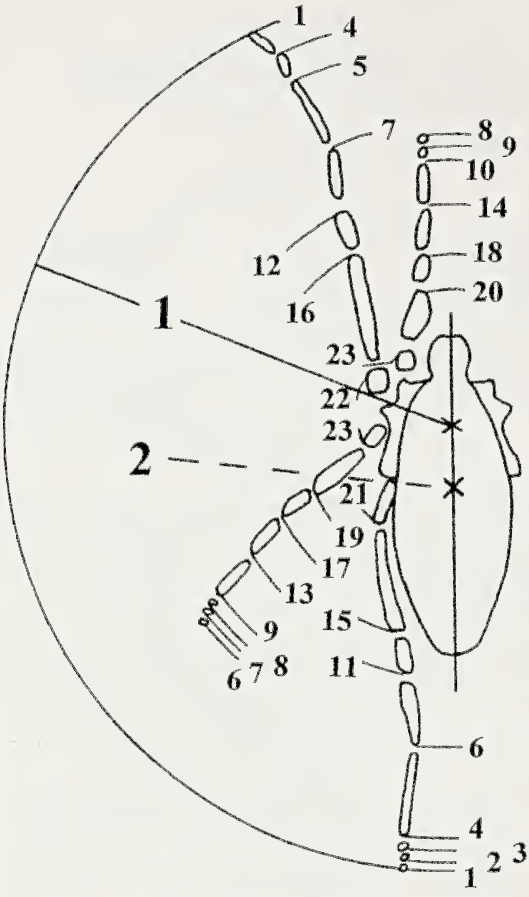

Figure 2.—The leg-centroid (1) and body-centroid (2) in *T. nepaeformis*. The range of danger risk, descending from 1 to 23, according to the leg-centroid.

first two leg pairs are a priori more exposed to physical dangers (Fig. 2). All leg articles (30 on each body side) were ranked into 23 classes of equally expected danger-risk, based on the radial distance of their distal parts from the leg centroid. For each leg, the correlation between the frequencies of injuries and the article lengths, and the expected risk and the realized frequencies of injuries was computed using the Pearson-product moment correlation. A chi square test was provided to analyze the differences between legs according to their injury frequencies. The computer software SPSS 11.0 (SPSS 2001) was used in all statistical procedures. The voucher specimens are deposited in the Slovene Museum of Natural History (Ljubljana).

RESULTS

In most populations, fewer than 5% of individuals were found injured. However, in three cases (Korte, Idrija, Tarcento) up to 20–30% of individuals had some injury. Fresh leg stumps were characterized by their ragged margins, and the healing ones by the brownish-black color of their injured tips. Article stumps reflecting old injuries, were of the usual color and with more or less regenerated, rounded tips. This way, in otherwise non-final articles (e.g., the 1st tarsus II, metatarsus and tibia), a smooth terminal chitin or a tip with a pseudonormal terminal-leg chaetotaxy, in some cases including an auxiliary claw, appeared. The final, damaged article was mostly shorter than the adequate opposite, undamaged one, but in a few cases elongation of the article was recorded. Regenerated damaged articles found in adults had most probably been severed in the juvenile and subadult stage. Some short articles, like the 1st, 3rd and 4th leg tarsi, were not injured.

Between–individual variation in nondirectional asymmetry of leg articles, except for trochanter II in females, was significantly larger than that of the measurement error (Table 1). On the other hand, the degree of asymmetry was larger than the degree of measurement error. We detected no evidence of DA; mean asymmetry in each trait was not significantly different from zero with an leptokurtic distribution, consistent with RA, but not with AS (Tables 2, 3).

The differences in R-L between sexes were not statistically significant in damaged specimens ($F_{1,94}$ = 0.01–3.79, P = 0.055–0.984); therefore the R-L data of both were pooled. The range of asymmetry in the lengths of the undamaged articles directly adjacent to the damaged ones was in 12 of 19 articles significantly larger in comparison to the undamaged specimens (Tables 2, 4, Fig. 3—case patella II), while tibia III shows a platykurtic distribution (g_2 = −5.7) (Table 3).

There was no significant correlation between the frequencies of injuries and the relative article lengths (r = 0.176, P = 0.352). As expected, the frequencies of injuries increased with increasing distance from the leg centroid (r = 0.970–0.995, $P < 0.001$). The frequencies of damage differed significantly between legs (chi square; $P < 0.001$), and de-

Table 1.—Mixed-model ANOVA of 14 leg characters (frequencies ≥ 3) of damaged legs in 67 randomly chosen individuals of *T. nepaeformis* chosen to analyze the measurement error.

	Male	Female
Leg article	*F*, *P*	*F*, *P*
Femur I	$F_{8,18} = 2.1$, $P = 0.045$	$F_{10,22} = 50.25$, $P < 0.0001$
Patella I	$F_{6,14} = 21.47$, $P < 0.0001$	$F_{9,20} = 13.9$, $P < 0.0001$
Tibia I	$F_{5,12} = 35.72$, $P < 0.0001$	$F_{2,20} = 52.08$, $P < 0.0001$
Trochanter II	$F_{13,29} = 32.69$, $P < 0.0001$	$F_{6,14} = 1.33$, $P = 0.618$
Femur II	$F_{14,28} = 5633$, $P < 0.0001$	$F_{6,14} = 227.1$, $P < 0.0001$
Patella II	$F_{9,21} = 41.12$, $P < 0.0001$	$F_{2,5} = 165.59$, $P < 0.0001$
Tibia II	$F_{8,19} = 55.38$, $P < 0.0001$	$F_{4,10} = 236.5$, $P < 0.0001$
Trochanter III	$F_{6,14} = 11.78$, $P = 0.0002$	$F_{3,8} = 19.93$, $P = 0.0009$
Femur III	$F_{5,12} = 36.77$, $P < 0.0001$	$F_{2,6} = 442.4$, $P < 0.0001$
Patella III	$F_{5,12} = 101.8$, $P < 0.0001$	$F_{2,6} = 34.0$, $P = 0.0001$
Tibia III	$F_{5,12} = 6.19$, $P = 0.0092$	No matches
Femur IV	$F_{3,9} = 39.63$, $P < 0.0001$	$F_{3,8} = 134.3$, $P < 0.0001$
Patella IV	$F_{3,9} = 126.78$, $P < 0.0001$	$F_{3,8} = 419.0$, $P < 0.0001$
Tibia IV	$F_{3,9} = 1295$, $P < 0.0001$	$F_{3,8} = 227.2$, $P < 0.0001$

creased from the 2nd, 1st, to the 3rd and the 4th legs (Tables 5, 6).

In the localities investigated for small mammals, hedgehogs were absent, and shrews were found to predate troguli: in 204 shrews, five opilionid and more than 14 other arthropod species were found. In two *Sorex araneus*, the remains of *T. nepaeformis* were recognized. No other predator of troguli was recorded, although moles and other occasional predators are believed to prey upon them, too.

DISCUSSION

While frequencies of less than 5% for leg damage in *T. nepaeformis* can have various causes, e.g., trampling, mechanical injury caused by falling stones etc., the larger percentage of injured individuals in other popu-

Table 2.—Kolmogorov-Smirnov's test (K-S) of distribution for normality and *t*-test for mean testing in *T. nepaeformis*. Levene's test of homogeneity of variances (One Way ANOVA: *F*, *P*) in undamaged and damaged specimens. (* $P < 0.05$; n.s. = no significant differences; / = no matches).

Leg article	K-S	*t*	*F*	*P*
Femur I	0.16 n.s.	−1.82 n.s.	0.60	0.439
Patella I	0.4 n.s.	−1.14 n.s.	42.54	<0.001
Tibia I	0.17 n.s.	0.20 n.s.	10.49	0.002
Metatarsus I	0.37*	−1.88 n.s.	14.50	<0.001
Trochanter II	0.24 n.s.	−0.13 n.s.	72.60	<0.001
Femur II	0.25 n.s.	0.34 n.s.	4.47	0.037
Patella II	0.23*	−0.91 n.s.	16.09	<0.001
Tibia II	0.32*	−1.15 n.s.	37.07	<0.001
Metatarsus II	0.17 n.s.	1.23 n.s.	30.80	<0.001
Trochanter III	0.27 n.s.	−1.10 n.s.	0.66	0.419
Patella III	0.19 n.s.	−0.71 n.s.	0.06	0.807
Tibia III	0.28 n.s.	−2.05 n.s.	19.85	<0.001
Metatarsus III	0.45*	−1.21 n.s.	35.46	<0.001
Tarsus III_1	0.38 n.s.	/	0.59	0.444
Tarsus III_2	0.25 n.s.	/	1.01	0.316
Femur IV	0.21 n.s.	−1.35 n.s.	0.18	0.674
Patella IV	0.21 n.s.	0.01 n.s.	39.08	<0.001
Tibia IV	0.27 n.s.	−0.01 n.s.	2.32	0.131
Metatarsus IV	0.23 n.s.	1.80 n.s.	59.12	<0.001

Table 3.—Statistical characteristics of leg articles length asymmetry in undamaged (n = 96) and damaged (n = 169) *T. nepaeformis*.

	Undamaged legs					Damaged legs					
Leg article	Mean	Variance	SE	Skewness	Kurtosis	n	Mean	Variance	SE	Skewness	Kurtosis
Trochanter I	0.008	0.002	0.005	0.225	−0.088	0					
Femur I	−0.027	0.006	0.008	−0.910	2.915	8	−0.055	0.007	0.030	−0.497	−1.199
Patella I	0.020	0.008	0.009	0.450	0.373	4	−0.212	0.139	0.187	−1.923	3.762
Tibia I	−0.005	0.005	0.007	−0.268	1.710	13	0.008	0.024	0.043	0.915	2.435
Metatarsus I	0.027	0.011	0.011	−0.315	0.552	13	−0.140	0.073	0.075	−2.544	6.698
Tarsus I1	0.002	0.001	0.003	−0.346	−0.204	1	−0.010				
Tarsus I2	0.008	0.001	0.004	−0.966	3.435	0					
Trochanter II	−0.003	0.004	0.006	0.106	0.237	10	0.167	0.141	0.119	1.391	1.248
Femur II	−0.035	0.005	0.007	0.131	−0.271	7	−0.003	0.017	0.050	−1.323	1.754
Patella II	0.014	0.014	0.012	0.049	0.779	26	−0.087	0.101	0.062	−1.228	3.550
Tibia II	0.005	0.005	0.007	0.207	0.578	15	−0.116	0.496	0.182	−1.336	3.504
Metatarsus II	0.057	0.015	0.013	0.612	1.030	17	0.060	0.181	0.103	−0.539	1.827
Tarsus II1	0.006	0.001	0.004	0.467	0.838	0					
Tarsus II2	0.012	0.004	0.006	1.496	4.152	0					
Trochanter III	−0.005	0.002	0.005	0.384	0.238	4	−0.045	0.007	0.041	−0.365	1.574
Femur III	−0.030	0.007	0.008	0.494	1.954	2	−0.065	0.014	0.085		
Patella III	0.023	0.012	0.011	0.104	0.376	6	−0.029	0.010	0.042	0.313	−0.571
Tibia III	0.009	0.018	0.014	−1.458	6.710	4	−0.375	0.133	0.183	0.002	−5.742
Metatarsus III	0.020	0.007	0.008	0.073	−0.444	7	−0.186	0.166	0.154	−2.609	6.852
Tarsus III1	0.003	0.001	0.003	0.276	−0.130	3	0.003	0.001	0.013	1.732	
Tarsus III2	0.004	0.001	0.003	−0.594	0.518	3	−0.017	0.000	0.009	0.935	
Tarsus III3	0.006	0.001	0.004	−0.333	0.971	0					
Trochanter IV	−0.014	0.004	0.007	0.095	0.419	2	0.074	0.017	0.091		
Femur IV	−0.017	0.009	0.010	0.198	1.286	4	−0.078	0.013	0.058	−0.803	0.659
Patella IV	0.052	0.018	0.014	−0.199	0.582	6	0.002	0.348	0.241	−1.250	1.818
Tibia IV	0.021	0.011	0.011	−0.366	1.712	6	−0.001	0.034	0.076	−1.699	3.286
Metatarsus IV	0.033	0.013	0.012	0.008	2.962	5	0.505	0.393	0.280	1.472	2.045
Tarsus IV1	0.009	0.001	0.004	−0.167	0.409	2	−0.005	0.001	0.025		
Tarsus IV2	0.010	0.001	0.002	−0.248	−0.403	1	−0.020				
Tarsus IV3	0.009	0.001	0.003	0.318	0.471	0					

lations might be the consequence of higher predation pressure. Short articles, like trochanter and most tarsal articles, were inappropriate in the analysis because of their low frequencies of injury, and higher level of measurement error, e.g., in a female trochanter II. The significantly larger RA in the damaged specimens, is assumed to be the direct consequence of the regenerative processes in the severed articles. Such damage has been recorded also in other *Trogulus* species.

Table 4.—Summary presentation of RA in legs of 169 damaged specimens of *T. nepaeformis* (+ = statistically significant differences; − = no significant differences; / = not taken into account). For abbreviations of leg articles, see Fig. 1.

Leg	Tr	Fe	Pt	Ti	Mt	Ta_1	Ta_2	Ta_3
I	/	−	+	+	+	−	/	
II	+	+	+	+	+	/	/	
III	−	/	−	+	+	−	−	/
IV	/	−	+	−	+	/	/	/

Table 5.—Frequencies of damaged legs in 169 *T. nepaeformis*.

	Males		Females		All	
Leg	n	n%	n	n%	n	n%
I	13	18.3%	26	26.5%	39	23.1%
II	33	46.5%	42	42.9%	75	44.4%
III	12	16.9%	17	17.3%	29	17.2%
IV	13	18.3%	13	13.3%	26	15.3%
Sum	71	100.0%	98	100.0%	169	100.0%

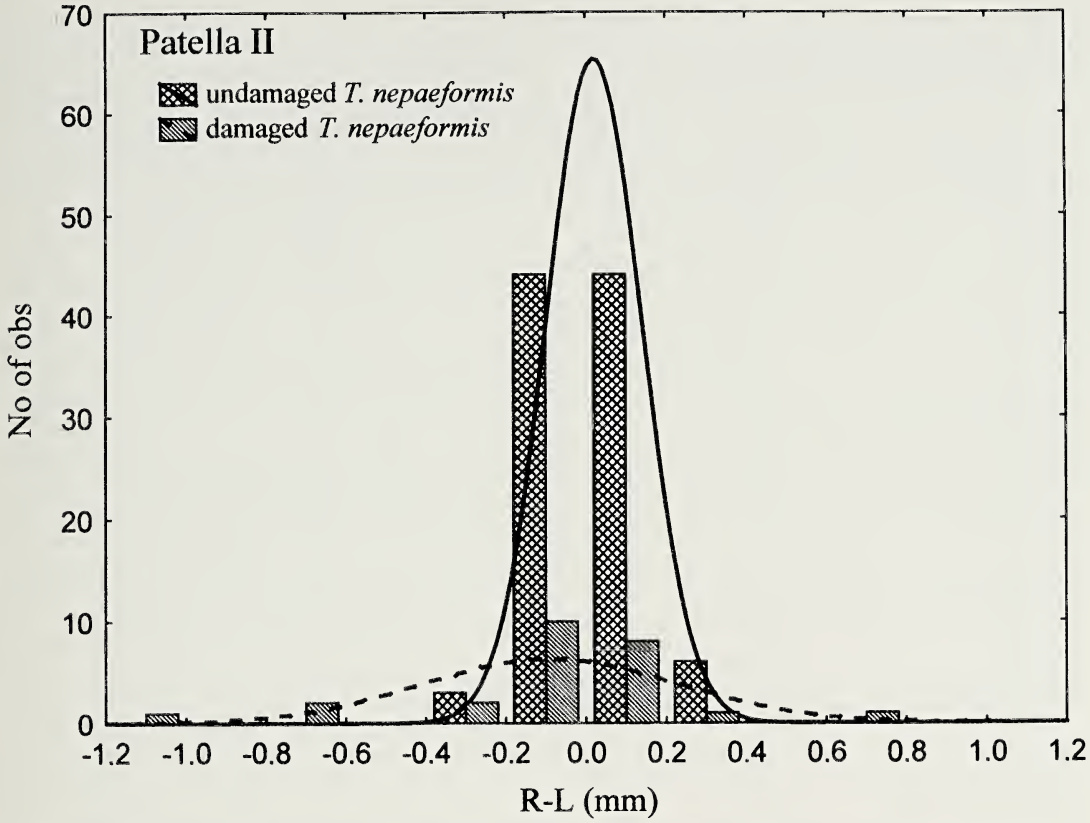

Figure 3.—Frequency distribution of R-L in patella II in damaged and undamaged *T. nepaeformis*.

In a few cases, elongation of the secondary end-article was recorded, resulting presumably either from fusion from the previous undamaged article with the rest of the damaged terminal one or by an anomalous repair. Ontogenetic abnormalities have rarely been reported in harvestmen, in Europe, e.g., by Hadži (1928) and Mitov (1995b). It seems likely that in *T. nepaeformis*, damage to the legs can induce anomalous growth in the stumps, especially during molting, a fact that could have been overlooked in other harvestmen.

The trochanter and the tarsal articles, except for tarsus II, are not appropriate for studying RA/FA in troguli because of their shortness and the consequent low frequencies of damage. There is no unequivocal explanation for the departure of tibia III in favor of AS, but this could be the consequence of the low frequency of occurrences of injury. As in *T. nepaeformis*, the injuries evoke measurement changes in the damaged, as well as in the previously undamaged articles.

The decreasing frequency of damage from the 2nd, 1st to the hind legs indicates that such injuries probably appear during the forward motion of troguli. It is assumed that most damage appears when troguli meet shrews within their common habitat while both are active. On such occasions, troguli normally simulate death and do not flee, thus minimizing total injury but receiving most injuries from the frontal side.

Probably the smooth, terminal chitin of the stump tips represents the first stage of regeneration, while the pseudonormal terminal-leg chaetotaxy and an auxiliary claw appear later. To confirm these interpretations, the regenerative process itself deserves to be studied in detail. This, and the role of harvestmen within the shrew diet will be analyzed elsewhere.

The influence of FA on mate choice has been found in a number of taxa (Uetz & Smith 1999). In night-active, ground inhabiting *T. nepaeformis* with small eyes, as well as in other edaphic harvestmen, vision has no important role. In *Trogulus* species, tactile and chemical senses promote the communication

Table 6.—Number of injured articles, cumulative number of injuries per leg, relative article lengths and range of danger risk per leg (descending from 1 to 23, according to the leg centroid) used in testing the stochasticity of injuries in *T. nepaeformis*.

Leg article	*n* of injured articles	Cumulative *N* of injuries/leg	Relative article length	Range of danger risk/leg centroid
Trochanter I	0	0	2	23
Femur I	8	8	5	20
Patella I	4	12	3	18
Tibia I	13	25	5	14
Metatarsus I	13	38	5	10
Tarsus I_1	1	39	1	9
Tarsus I_2	0	39	1	8
Trochanter II	10	10	3	22
Femur II	7	17	14	16
Patella II	26	43	5	12
Tibia II	15	58	6	7
Metatarsus II	17	75	9	5
Tarsus II_1	0	75	3	4
Tarsus II_2	0	75	3	1
Trochanter III	4	4	3	23
Femur III	3	6	8	19
Patella III	6	12	4	17
Tibia III	4	16	5	13
Metatarsus III	7	23	5	9
Tarsus III_1	3	26	1	8
Tarsus III_2	3	29	1	7
Tarsus III_3	0	29	1	6
Trochanter IV	2	2	5	21
Femur IV	4	6	13	15
Patella IV	6	12	4	11
Tibia IV	6	18	8	6
Metatarsus IV	5	23	11	4
Tarsus IV_1	2	25	1	3
Tarsus IV_2	1	26	1	2
Tarsus IV_3	0	26	1	1

between sexes Pabst (1953). Troguli pose the opportunity to study the influence of RA on tactile and chemical cues interacting between sexes.

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WOLF SPIDER (ARANEAE, LYCOSIDAE) MOVEMENT ALONG A POND EDGE

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ABSTRACT. Wolf spiders (Araneae, Lycosidae) are important predators at freshwater-forest ecotones where their distribution may be determined by their ability to respond to, amongst other factors, moisture and prey levels. The purpose of this study was to examine the movement of wolf spiders along a pond-forest boundary at Mountain Lake Biological Station, Virginia. We performed two mark-recapture studies at two temporal and spatial scales (4 h–20 d and 1 m–~20 m, respectively) to determine the probability of movement by the spiders. Mark-recapture studies are useful for measuring individual movement, but, because of the difficulty of marking small arthropods, are not often used for spiders. This mark-recapture study showed the spiders moved very little over the temporal and spatial scale used: 0–54% per day chance of moving to the adjacent 1-m^2 plot around the pond and 0–2% per day chance of moving to the adjacent 1-m^2 plot to and from the pond. This finding is in contrast to other studies that have shown wolf spiders to completely exit a 900-m^2 quadrant within several days. We discuss possible causes of this low mobility and its implications for wolf spider distribution and abundance at the pond edge.

Keywords: Mark-recapture, freshwater ecotone, Pollock's robust model

Animals move to find favorable physical conditions, food and mates, for dispersal and to avoid predation (Jones 1977; Henschel 2002; Ramos et al. 2004). Both empirical and theoretical studies have long recognized that the effect of an abiotic or biotic factor on the distribution of an organism is greatly influenced by the scale over which that organism moves (Cain 1985; Hanski 1998; Weins 2001). Understanding the ability and propensity for individuals to move is, therefore, a prerequisite for predicting the response of a species to changing resources and physiological conditions (Morse 2000; DeVito et al. 2004). The usefulness of mark-recapture methods for estimating population parameters are well-known (Nichols 1992), but are not often used to quantify movement of small arthropods.

Habitat boundaries are common in nature. These boundaries or interfaces offer a large amount of variation in biotic and abiotic factors. At the freshwater-terrestrial interface, moisture and food have been shown to vary and may influence the distribution of various consumers (spiders: Graham et al. 2003; Power et al. 2004; beetles: Hering & Platchter 1997; birds: Murakami & Nakano 2002). For example, a decline in lizard population density has been observed near a river's edge when the inputs of aquatic insect prey are experimentally reduced (Sabo & Power 2002). At a freshwater pond edge, moisture had a positive association with 3 of the 4 spider species measured (Graham et al. 2003). At the edge of a forest stream, a connection was found between flooding frequency and litter habitat, which affected the stratification of spiders along the edge (Uetz & Unzicker 1976). Information about movement gives insight into the relative importance of these factors in driving the abundance and distribution of consumers at freshwater-terrestrial interfaces.

Spiders are found in high densities in most terrestrial habitats (Moulder & Reichle 1972), and many live near aquatic-terrestrial interfaces (Nørgaard 1951; Kato et al. 2003; Kraus & Morse 2005). At this interface, moisture and desiccation tolerance are important factors influencing wolf spider distribution (DeVito & Formanowicz 2003; Graham et al. 2003). Some wolf spiders species, including repre-

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sentatives of the genus *Pirata*, which are found in our study area, can walk and therefore hunt on water as easily as on land (Foelix 1996).

Aquatic insects can also influence the distribution of wolf spiders near the water's edge (Henschel et al. 2001; Power et al. 2004; Kraus 2006). Wolf spiders prey on flies and other small invertebrates in the riparian zone including aquatic insects that emerge onto land (Henschel et al. 2001). The life stage, sex and physiological constraints of the spider, however, strongly affect its ability to respond to changes in prey availability (DeVito et al. 2004; Power et al. 2004). Male wolf spiders are often more active than females when searching for a mate (Framenau 2005), while juvenile fishing spiders move more frequently than adults to search for food (Kreiter & Wise 1996). Finally, spider species that desiccate more easily are constrained to certain microhabitats, and thus their movements should be limited to these habitats (Devito et al. 2004).

The purpose of this study was to determine the scale and pattern of wolf spider movement in response to differences in the biotic and abiotic environment that occur around a small pond. This was accomplished by monitoring the movement of wolf spiders (Araneae, Lycosidae) in the area surrounding a small pond in the southern Appalachians. We used mark-recapture to track cohorts > 0–3 m from and > 0–20 m around the pond perimeter. We hypothesized that the spiders would move laterally around the pond, but not much away from or towards the pond due to their close association with water.

METHODS

Study site and sampling design.—The study was conducted around a pond at the Mountain Lake Biological Station in the Allegheny Mountains of southwestern Virginia (37.38°N, 80.52°W, elev. 1,160 m). The shallow pond in our study site, Sylvatica (70 m perimeter) was fishless. The edge of the pond was fairly well defined. There was a grassy area directly surrounding the pond and beyond that was forest, with mainly oaks (*Quercus alba*, *Q. rubra*) and pines (*Pinus rigida*). The common wolf spider species found at this study site include *Pirata cantralli* Wallace & Exline 1978, *Pirata montanus* Emerton 1885, *Pirata sedentarius* Montgomery 1904, *Pardosa milvina* Hentz 1844 and *Pardosa moesta* Banks 1892. Voucher specimens have been deposited at the Smithsonian National Museum of Natural History, Washington, DC, USA. *Pirata cantralli* and *P. sedentarius* both appear to be water specialists (DeVito & Formanowicz 2003; this study), while *P. milvina* inhabits open habitats (Marshall et al. 2000) and *P. moesta* has more general affinities including forested and wet areas (Buddle 2000). *Pirata montanus* lives in leaf litter (Pearce et al. 2004), and in this study was constrained to one area of the pond where the slope aspect was steep and trees and shrubs grew closer than 3 m from the water's edge.

We performed an initial mark-recapture analysis to find the approximate detection probability. In each of two 1 m^2 plots, LA visually searched for wolf spiders for 20 minutes, marked, released and waited one hour before searching again. We found a 15% detection probability in one plot and 26% in the other. While this was lower than some recapture rates for wolf spiders (Framenau & Elgar 2005, > 30% recapture rate), it is comparable to the recapture rate found by Kiss & Samu (2000) (5–19% recapture rate), and is high enough to estimate movement probability with sufficient accuracy. To test that the plot remained a closed system during the 1 h before recapture, one of us (LA) visually monitored three wolf spiders (one female with egg sac, one adult male, and one juvenile) for 0.5 h and found that each moved 8 cm or less.

We estimated movement rates of wolf spider cohorts using two randomly placed grids that were comprised of nine rectangular or square plots each located around Sylvatica Pond (Fig. 1). "Dispersed Grid" (D1-D3, Figure 1), begun 14 June 2004 at the northeast side of the pond, had nine plots split into three separate columns. Each column consisted of three 1 × 3-m plots located adjacent and parallel to the pond edge. Movements between plots in a column therefore required that the spiders moved at least > 0–3 m. Columns were 8–11 m apart, requiring spiders to move at least 8–28 m to reach another column. They were equidistant from existing structures from another study (Kraus 2006). "Adjacent Grid" (A on Fig. 1), begun 28 July 2004 on the northwest side of Sylvatica Pond, consisted of nine adjacent 1 × 1-m plots, set in a square formation. In this case, for spider movement

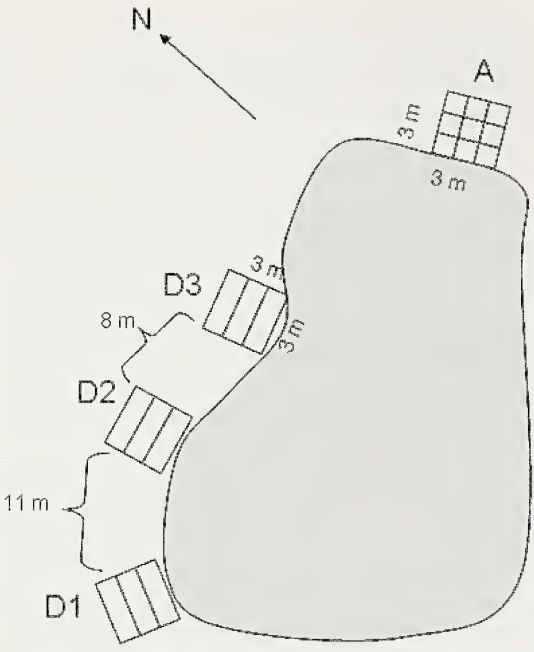

Figure 1.—Diagram of Sylvatica Pond. The two grids, each containing 9 plots, represent the plots used for the mark and recapture of this study (A, D1-D3). The plots of "A" (Adjacent Grid) are 1 × 1 m and the plots for "D" (Dispersed Grid) are 1 × 3 m.

perpendicular or parallel to the pond edge to be detected, spiders had to move at least > 0–3 m. The Adjacent Grid mark-recapture was done after the entire mark-recapture study for Dispersed Grid was completed. Dispersed Grid detected no long distance movement of spiders around the ponds, so we decided to arrange the Adjacent Grid plots in a close adjacent pattern to determine if movement occurred at a smaller scale.

We used Pollock's (1982) robust mark-recapture sampling design with three primary (long) sampling periods (for Dispersed Grid: 1, 5 and 25 d; for Adjacent Grid: 1, 4 and 8 d), each containing two secondary (short) sampling periods (morning and afternoon of each primary sample date), to estimate movement probability while taking into account variation in detection probability at different sample times. Due to the abundance of spiders in the study area and the difficulty in uniquely marking individuals of such small size (<10 mm in length), we performed our study on spatial cohorts of animals (one per plot), which limited the number of colored marks to 5 per animal. In the morning of day one of sampling for Dispersed Grid we systematically hand-searched each of the nine plots for 20 min, collecting as many wolf spiders as possible. The searches were started on the perimeter of each plot to limit the number of spiders chased out. The intense searches may have caused slight disturbance to the plots, but there was evidence in this system that searching would yield more spiders, especially of sedentary *Pirata* species than passive trapping (Kraus 2006). Spiders from each plot were marked with a different color of non-toxic model paint on their abdomen so we were able to estimate cohort movement rates. The spot was made with the blunt end of a dissecting needle so it would be small enough to not impede their movement or increase predation on the spider. We have some evidence that we were fairly successful achieving these objectives although survival rates increased by about 10% after the first primary period, indicating some mortality may have been caused by the marking process (see Results). The spiders were released around noon. That afternoon the plots were searched again, for 20 min in each plot. These spiders were recorded, marked a different color and released. We repeated the procedure on day five and day twenty-five. Each spider received a maximum of five spots, with each sampling period and plot having a different color. For Adjacent Grid, we used the same Pollock's Robust design but LA searched alone for 10 min instead of 20 min in each plot, because of the smaller size of the plots and the relatively good capture probability (12–74%).

Data analyses.—Mark-recapture data were analyzed using Program MARK (Version 4.0, downloaded July 2004; White & Burnham 1999). Due to small sample movement rates among plots, which disallowed individual estimates of movements between each plot, each grid was condensed laterally such that vertical (away from and towards the ponds) movement rates of spiders could be estimated and condensed vertically such that lateral (around the perimeter of the ponds) movement rates of spiders could be estimated. We used the Multistrata recapture setting in MARK, because on a few occasions there was movement within a primary period, which violates an assumption of Pollock's Robust design. All analyses are therefore performed within the

Multistrata framework; the language used to describe sampling intervals in the results section reflects this switch. Survival (s) is the probability of survival from one recapture event to the next, capture probability (p) is the probability of capturing an individual given that the individual is in the plot, and transition probability (ψ) is the probability of moving from one sample plot to the next. The variable "t" refers to the time between recapture events in days and "d" refers to the linear distance in meters between sample plots.

Our most fully specified model, $p(\cdot)s(\cdot)$, made the simplifying assumption that survival and recapture probabilities would be constant across short sampling intervals and across long sampling intervals within each grid type (dispersed vs. adjacent, see above). We predicted that these assumptions would be valid if movements were small and if survival was similar over the month of sampling. We did not expect movements of all species to be small based on another movement study (Kiss & Samu 2000). However, data on desiccation rates did suggest that *Pirata* species might be constrained to living near the pond edge (Devito et al. 2004), which could limit movement. It seemed probable that survival would be similar over the study since the number of reproductive adults at this site is still increasing at this point in the season (J.M. Kraus, unpublished data).

Based on the fully specified model, we developed four additional models, which constrained movement probabilities in different ways. We varied the parameters in this way to determine the role time and distance played in modeling spider movement. We predicted that distance and time would play a role, but only if movement was limited. First, we constrained movement to be constant by both time and distance, $p(\cdot)s(\cdot)\psi(\cdot)$, essentially saying that the distance between plots did not make a difference to the probability that a spider would move that distance and that the length of time a spider had to move did not affect the probability it would move.

The second model constrained movement to be constant by distance but not time, $p(\cdot)s(\cdot)\psi(\cdot, t)$. The probability of movement between the longer distances was constrained to be the same as the probability of movement between shorter distances. The probability of movement, however, was different for shorter periods of time (3 h) than longer periods of time (5 or 25 d). In the third model movement was constrained to be constant by time, but not distance, $p(\cdot)s(\cdot)\psi(d, \cdot)$. The length of time a spider had to move did not affect the probability it would move. The distance a spider had to move did affect the probability that it would move that distance. In the fourth model movement was not constrained by time or distance: the probability of moving was allowed to be different for long versus short distances and long versus short sampling intervals, $p(\cdot)s(\cdot)\psi(d, t)$.

We tested the assumption that capture probabilities were constant between sampling periods (i.e., not time variable) with a final model that constrained movement and survival, but not capture probability, $p(t)s(\cdot)\psi(\cdot)$. These models were each applied to the four sets of condensed data (Dispersed Grid vertically condensed, Dispersed Grid laterally condensed, Adjacent Grid vertically condensed, and Adjacent Grid laterally condensed), and then we used Akaike's Information Criterion corrected for small sample size (AIC_c, Akaike 1985) to choose the best-fit model.

RESULTS

A total of 499 spiders with 105 different capture histories were found and marked in Dispersed Grid. Of these, 80% were *P. cantralli*, 10% were *P. sedentarius*, 7% were *P. milvina* and the remainders were *P. montanus* and *P. moesta*. Forty-three percent of wolf spiders marked were juveniles, 28% were females, 17% were males, and 12% were females with egg sacs. Adjacent Grid yielded 147 spiders with 74 capture histories. The majority of spiders in Adjacent Grid were *P. cantralli* (83.7%). The remaining spiders were 6.8% *P. montanus*, 5.4% *P. milvina*, 3.4% *P. moesta*, and 0.7% *P. sedentarius*. Adjacent Grid had mainly female and juvenile spiders; 31.3% were juveniles, 25.9% were females with egg sacs and 36.7% were female spiders. The remaining 6.1% were males. The number of captures per species, sex within species, and developmental stage was not great enough to separately analyze the movement of each group. All species were analyzed together with the understanding that results are presented for the wolf spider assemblage as a whole but mainly reflect the movement of *P. cantralli*. When the data were condensed lat-

Table 1.—Mean (± s.e.) survival (s), capture (p) and movement probabilities (ψ) over entire sampling for Dispersed Grid examining movement to and from the ponds (condensed laterally) with a sample size of 499 spiders. Sampling interval is the time between release of spiders and searching the plots again. The AIC_C score is 980.61, the next best model has an AIC_C score of 983.35.

	Short sample intervals (3 h)	Long sample intervals (5 d and 25 d)
s	0.69 ± 0.08	0.95 ± 0.01
p	0.36 ± 0.05	0.24 ± 0.04
ψ (adjacent plots)	0.05 ± 0.02	0.06 ± 0.03
ψ (non-adjacent plots)	0.00 ± 0.00	0.05 ± 0.03

Table 2.—Mean (± s.e.) probability of movement (ψ) for Adjacent Grid examining movement around the ponds (condensed vertically) with a sample size of 147 spiders. Sampling interval is the time between release of spiders and searching the plots again. The AIC_C score is 492.54, the next best model had a score of 498.28.

Sampling interval	Adjacent plots	Non-adjacent plots
1 (3 h)	0.03 ± 0.03	0
2 (4 d)	0.13 ± 0.12	0
3 (3 h)	0	0
4 (4 d)	0.22 ± 0.10	0
5 (3 h)	0.13 ± 0.10	0

erally for Dispersed Grid the number of different capture histories observed decreased to 70 and when condensed vertically it decreased to 62. The laterally condensed data for Adjacent Grid had 62 different capture histories and the vertically condensed data had 43. All probabilities are presented as daily estimates.

The four data sets had different best-fit models. For Dispersed Grid examining movement around the pond (condensed vertically), the best model was $p(\cdot)s(\cdot)\Psi(\cdot)$. For this model the probability of moving between columns (at least 8–28 m) was 0, while average survival probabilities were high (survival probability across shorter sampling intervals p ± s.e. = 0.77 ± 0.09 and survival probability across longer sampling intervals = 0.93 ± 0.01) The capture probability was unconstrained in this model and ranged from 12–72% for all sample period-plot combinations. Sampling Interval 4 (25 d) had a slightly higher capture probability, although the highest single capture probability was in Interval 1 (3 h); Interval 5 (3 h) also has a high capture probability. There does not seem to be any pattern in the capture probability rates. For Dispersed Grid examining movement to and from the pond (condensed laterally), the best fit model was $p(t)s(\cdot)\psi(d, t)$, which allowed movement across short sampling intervals to be different from movement across long sampling intervals and also let movement between adjacent rows be different from movement between nonadjacent rows. The probability of moving between rows (in this case > 0–3 m) was small ($p < 0.06$) for all four possibilities (Table 1).

The best-fit model for Adjacent Grid examining movement around the pond (vertically condensed) was $p(\cdot)s(\cdot)\psi(\cdot)$. This model constrained capture probabilities and survival to be constant across short and long sampling intervals. The survival was high across short sampling intervals (s ± s.e. = 0.77 ± 0.10) and across long sampling intervals (s ± s.e. = 0.88 ± 0.04). The higher survival across the longer sampling period might reflect increased mortality due to the marking procedure in the short term. The capture probability p (± s.e.) across short sampling intervals was 0.50 (± 0.07) and across long sampling intervals was 0.34 ± 0.07. The probability of horizontal movement for Adjacent Grid was higher than all estimates of movement in the Dispersed Grid and estimates of vertical movement in the Adjacent Grid (Table 2). For Adjacent Grid examining movement to and from the pond (condensed laterally), two models were equally well fit, $p(\cdot)s(\cdot)\psi(\cdot)$ and $p(\cdot)s(\cdot)\psi(d, \cdot)$, with AICc values only 0.04 apart. For both models survival, capture probability, and movement were constrained to be constant across short sampling intervals and constant across long sampling intervals. However, the probability of movement between adjacent rows (> 0–2 m) was allowed to be different from the probability of movement between nonadjacent rows (> 1–3 m) for one but not the other model. For both models the survival was high and the same; the capture probability (p) was the same for both as well, and the probability of movement (> 0–3 m) was between 0.01 and 0.04 (Table 3).

Table 3.—Survival, capture probability and probability of wolf spider movement for Adjacent Grid examining movement to and from the pond (condensed laterally) with a sample size of 147 spiders according to two equally fitting models. Sampling interval is the time between release of spiders and searching the plots again. Means ± s.e. are given. The AICC score for the first model is 459.35, the second model's AICC score is 459.39, the third best fit model is 461.28.

	Short sample intervals (3 h)	Long sample intervals (4 d)
Model: $p(.)s(.)\psi(.)$		
Survival	0.77 ± 0.10	0.88 ± 0.04
Capture probability	0.50 ± 0.07	0.34 ± 0.07
Probability of movement	0.02 ± 0.01	0.02 ± 0.01
Model: $p(.)s(.)\psi(d, .)$		
Survival	0.77 ± 0.10	0.88 ± 0.04
Capture probability	0.50 ± 0.07	0.34 ± 0.07
Probability of movement between adjacent plots	0.04 ± 0.02	0.04 ± 0.02
Probability of movement between nonadjacent plots	0.01 ± 0.01	0.01 ± 0.01

DISCUSSION

In this study, we made two independent estimates of wolf spider movement near Sylvatica Pond. The first, taken from Dispersed Grid, estimated movement 0–3 m to and from the pond and 8–28 m around the pond edge 3 h, 5 d, and 25 d after marking. The second, taken from Adjacent Grid, estimated movement 0–3 m to and from the pond and 0–3 m around the pond edge at 3 h and 4 d after marking. The first estimate suggests spiders had a 0% chance of moving 8–28 m around the pond at all of the time scales used (< 25 d). On the other hand, spiders had a 5–6% chance of moving 1–2 m to and from the pond over 5 or 25 d (but 0% chance of doing so in 3 h). The second estimate suggests that spiders had a 4% chance of moving between adjacent rows (0–2 m) to and from the pond over 3 h or 4 d, but no chance of moving among non-adjacent rows (> 1–3 m). Chances of moving between columns around the pond (0–2 m), however, averaged 5% over 3 h, and 18% over 4 d (calculated from Table 2). Although we detected a relatively small amount of movement in our spiders, infrequent longer-distance movements are probably underestimated (Samu et al. 2003).

We predicted that lateral movement around the pond would be much greater for these spiders than movement to and from the pond due to moisture constraints (DeVito and Formanowicz 2003; Graham et al. 2003). We discovered that movement around the pond was more probable than movement to or from the pond (up to 18% vs. 4%), but that movements of over 3 m were rare enough to be undetected within the study. Higher movement around than to and from the pond fits what is known about the high desiccation rates of wolf spiders that specialize in habitats near water (e.g., *P. sedentarius*, DeVito et al. 2004), and the importance of aquatic prey to spiders living near freshwater (Kato et al. 2003; Power et al. 2004). However, even taking these limitations into account, the probability of moving distances as short as 0–2 m around the pond edge was relatively small compared to previous estimates of wolf spider movement (Morse 1997; Kiss & Samu 2000). For example, Kiss & Samu (2000) found that marked wolf spiders had completely exited a 900 m^2 quadrant over several days of trapping near Hungarian alfalfa fields. Morse (1997) also found that intertidal wolf spiders (*Pardosa lapidicina* Emerton 1885) migrating with the tide could move the width of the beach (up to 25 m) in one tidal cycle. However, those spiders that remained in the supratidal on the high beach moved infrequently, employing a sit-and-wait hunting strategy. Cages that were located around our study pond from another study likely impeded the long distance movement of the spiders. However, anecdotal evidence (see below) suggests this impediment most likely only affected *P. milvina*, and not the majority of marked spiders in this study (*P. cantralli*).

Wolf spiders are generally thought of as active hunters. Most do not construct webs to catch prey. Our data show that the spiders in

this study, the majority of which was represented by the water specialist *P. cantralli*, apparently hunt in a small (<1 m) region. However, there was some anecdotal evidence that another common species at the pond is capable of larger scale movement. On one occasion, a marked *P. milvina* was found to have moved at least 7 m around the pond perimeter over a five week time period. *Pardosa milvina*, which is found in early successional habitats and is a good colonizer (Marshall et al. 2000), appears to move more than *P. cantralli* and may be able to track resources over a larger spatial scale around the pond.

Several abiotic and biotic factors including moisture and prey distribution can influence the ability or propensity of wolf spiders to move (Nørgaard 1951; Humphreys 1975). Desiccation tolerance and moisture levels limit the distribution of wolf spiders around ponds (DeVito & Formanowicz 2003; Graham et al. 2003). Furthermore, Kreiter & Wise (2001) found that adult female fishing spiders that have been fed move less frequently than those who have not received a meal. Perhaps those spiders living near the pond edge receive sufficient prey from aquatic sources and therefore may not need to roam. There are differences in the soil moisture and prey abundance in areas around the pond (Kraus 2006; L. Ahrens & J.M. Kraus, unpublished). Such differences may dictate where the spiders are able to hunt for food as well as their abundance within those limits. While probability of movement was not analyzed specifically for the differences in life cycle due to small sample size, further study on these differences could provide useful information about which spiders are most responsible for movement. Movement of wolf spiders is most likely affected, therefore, by a combination of biotic and abiotic factors that pose constraints on the distribution and abundance of wolf spiders at the pond edge.

The spatial scale chosen for this study may have had a large impact on the findings from the model. A scale too large or too small can cause important movement and community interactions to be missed (Kareiva 1990). Our study on wolf spiders was conducted to determine movement at the scale of meters during the summer months, fitting the size of the ponds and the active period of the spiders. A study done over a longer time period or a smaller scale may reveal seasonal or more local movement patterns.

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MICROHABITAT USE BY THE WHIP SPIDER *HETEROPHRYNUS LONGICORNIS* (AMBLYPYGI, PHRYNIDAE) IN CENTRAL AMAZON

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ABSTRACT. We investigated microhabitat selection in the Amazonian whip spider *Heterophrynus longicornis* (Butler 1973). The probability of finding individuals of this species increased according to the diameter of the trees. Moreover, there was a positive correlation between the size of adult individuals and the diameter of the trees on which they were found. Our results also provide quantitative support for a previous suggestion that *H. longicornis* prefers large trees bearing buttresses and burrows at the base where the individuals hide during daytime. Since whip spiders prefer large trees, the anthropogenic disturbance promoted by selective logging or the degeneration of the forest structure due to fragmentation and edge effect may have a negative effect on the spatial distribution and, consequently, on the density and population ecology of *H. longicornis*.

Keywords: Brazil, buttress, conservation, ecology, habitat selection, trees

The selection of habitat may have major consequences for the biology of an organism since it will influence the range of abiotic conditions and biotic interactions that the organism encounters (Sih et al. 1992). Individuals that select appropriate habitats may have access to shelters with appropriate thermal, hydric, and structural conditions, as well as sites in which they can maximize the chances of finding prey and sexual partners, and minimize the encounters with competitors and predators (Martin 2001). Several arachnids are known to exhibit precise habitat selection, and this behavior has been demonstrated to have a positive effect on the fitness of the individuals (e.g., Fritz & Morse 1985; Lubin et al. 1993; Morse & Stephens 1996; Goldsbrough et al. 2004).

The order Amblypygi comprises over 120 species, commonly known as whip spiders, which are widely distributed in the warmer tropical regions of the world (Weygoldt 2000). Representatives of the order have a dorso-ventrally flattened body, well-developed pedipalps bearing spines that are used for prey capture, and a long first pair of legs with sensory function. Most species are nocturnal and live in moist forests where they are found under rotting logs, between rock breaches, and inside caves (Weygoldt 2000). Recently, Hebets (2002) demonstrated that individuals of the whip spider *Phrynus parvulus* Pocock 1902 select microhabitats based on the tree surface, moss cover, and the presence of buttressing. In this study, we investigated if individuals of the Amazonian whip spider *Heterophrynus longicornis* (Butler 1973), which are commonly observed on the bark of large trees and inside natural cavities in fallen logs (Beck 1968; Weygoldt 1972a, 1977), also exhibit microhabitat selection.

The study was conducted during July 2004 in the Reserve 1501, also known as Km 41 (2°24′S, 59°44′W), a continuous "terra firme" (upland) forest that is one of the controls of the Biological Dynamics of Forest Fragments Project (BDFFP) in Central Amazon, nearly 80 km north of the city of Manaus, northern Brazil. The altitude in the reserve ranges from 50 to 150 m, and rainfall varies from 1900 to 2500 mm annually, with a dry season from June to October. For a detailed description of the area see Lovejoy & Bierregaard (1990).

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We used the 100 × 100 m network of trails in the reserve to establish five transects 4 m wide and ranging from to 150 to 350 m in length. Along the transects we actively searched for the whip spiders on fallen logs and tree trunks up to 2 m of each side of the trails, so that the total sampled area was 6,628 m^2. Each transect was searched only once and the samples were conducted in five consecutive nights (between 20:00–01:00 h). We searched for whip spiders by scanning every tree with a diameter at breast height (DBH) ≥ 10 cm, from nearly 2 m down to the ground, which seems to be the foraging range of large whip spiders (Stewart & Woolbright 1996). All adult and subadult individuals were captured, sexed, and the cephalothorax width was measured with calipers. After manipulation, we returned the individuals to their original location and the trees where they were found were marked with a colored tag. The juveniles were not captured because they are very fragile and could be injured during the manipulation. For all individuals, we measured their height on the tree trunks using a tape measure and recorded their position on the bark surface according to three categories: facing downwards, facing upwards or parallel to the ground. Voucher specimens are deposited in the Museu de História Natural da Universidade Estadual de Campinas (ZUEC, Brazil) and Museu de Zoologia da Universidade de São Paulo (MZSP, Brazil).

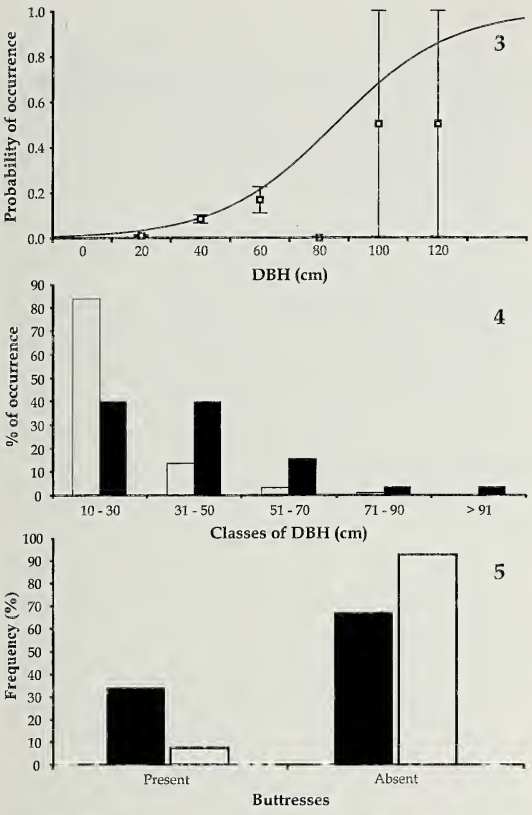
In the morning after each sampling, we measured the DBH of all trees inside the transects, making a distinction between those on which *H. longicornis* were present versus those on which they were absent. We also scored the trees as positive or negative when buttressing was present or absent, respectively. Logistic regression was performed to determine whether the diameter of the trees could predict the absence (0) or presence (1) of *H. longicornis*. A Kolmogorov-Smirnov test was performed to compare the distribution of classes of DBH in trees with and without *H. longicornis*. The correlation between the size of the whip spiders (considering only subadults and adults) and the DBH of trees on which they were found was tested using a Spearman rank correlation. A chi-square goodness-of-fit was used to test the null hypothesis that the frequency of occurrence of individuals was independent of the presence of buttresses. The expected values were generated based on the proportion of buttressing trees in our five transects.

We sampled a total of 703 trees with DBH ≥ 10 cm, and on 31 we found individuals of *H. longicornis*. From the 46 individuals that were seen, 11 were juveniles in different stages of development, 10 were females (including three bearing egg sacs), and 25 were males. The size of the males ranged from 9.2 to 14.9 mm (mean ± SD = 12.4 ± 1.2 mm) and the size of the females ranged from 9.2 to 12.6 mm (10.7 ± 1.3 mm). Thirteen individuals (five females, six males, and two juveniles) were found on fallen logs and in all cases there were large cavities in these logs that were used as diurnal shelters. Thirty-three individuals (six females, 19 males, and eight juveniles) were found on the bark of living trees, 80.6% of which possessed burrows at their base that were also presumably used as diurnal shelters. Only two trees presented more than one individual: in one case they were a juvenile and a female, and in another case they were a male and a female. No intraspecific interaction was observed in the field.

The height of the individuals on the tree trunks ranged from 18 to 160 cm (77.2 ± 41.1 cm). The great majority of the individuals (78.3%) were facing downwards, and the remaining were facing upwards (8.7%) or parallel to the ground (13.0%). Amongst those facing downwards, it was common to observe individuals with the pedipalps raised and widely opened, in a typical hunting posture (Fig. 1). Two individuals were found consuming prey: a juvenile ate a cockroach and a female ate a ctenid spider (Fig. 2).

The probability of finding individuals of *H. longicornis* increased according to the DBH of the trees (Fig. 3). Nearly 80% of the trees in the transects had a DBH between 10 and 30 cm, but only 45% of the whip spiders were found in trees of this size category (Fig. 4). Thus, the distribution of classes of DBH in trees with and without *H. longicornis* was markedly different (Kolmogorov-Smirnov test, $\chi^2 = 27.07$; $d.f. = 2$; $P < 0.001$). There was a positive correlation between the size of the adult individuals and the DBH of the trees where they were found ($r_s = 0.523$; $n = 24$; $P = 0.008$). Finally, buttressing trees presented more individuals of *H. longicornis* than expected by chance (Fig. 5).

Figures 1–2.—1. Adult female of *Heterophrynus longicornis* in a typical hunting position facing downward on a tree trunk in Central Amazon; 2. Female of *H. longicornis* preying on a ctenid spider that climbed the tree trunk at night (photos by G. Machado).



Figures 3–5.—3. Logistic regression showing the increase in the probability of finding individuals of *Heterophrynus longicornis* according to the increase in the DBH of the trees in a continuous forest in Central Amazon (χ^2 = 28.79; *d.f.* = 1; $P < 0.001$). In order to facilitate visualization, the DBH measurements were divided into classes and the data on presence (1) and absence (0) of whip spiders are presented as mean ± SD for each class; 4. Distribution of classes of DBH of trees with (black bars) and without (white bars) individuals of *H. longicornis*; 5. Percentage of trees occupied (black bars) or not (white bars) by individuals of *H. longicornis* according to the presence of buttresses (Yates corrected, χ^2 = 44.00; *d.f.* = 1; $P < 0.001$).

Our results provide quantitative support for the previous suggestion of Weygoldt (1972a) that *H. longicornis* prefers large trees bearing buttresses and presenting burrows at their base where the individuals hide during daytime. According to this author, this preference may be explained because buttresses provide shelters for the whip spiders. Working with *Phrynus parvulus* in a rain forest from Costa Rica, Hebets (2002) also showed that the individuals prefer large trees with buttresses, but no explanation for such a pattern was provided. It is very common that buttressing trees accumulate a great amount of leaf litter at their base, and this microhabitat is used by many groups of invertebrates and vertebrates as shelter (e.g., Voris 1977; Cabanillas & Castellón 1999; Whitfield & Pierce 2005). It is possible that the whip spiders prey on individuals that leave the litter at night and climb on the trees. Indeed, the fact that most individuals of *H. longicornis* were found facing downward suggests that they were waiting for ascending prey. Additionally, the large flat area of buttressing could also provide an arena for courting, but Hebets (2002) showed that the choice of large buttressing trees by *P. parvulus* is not sex-specific.

Adult individuals of many species of whip spiders are territorial, and this is particularly pronounced in the males, which use formalized fights for defending their territories (Weygoldt 2000). In *H. longicornis*, a male and a female, and sometimes a whole family with small juveniles were found in the same tree hole (Weygoldt 1977). However, agonistic behavior between males of the same reproductive stage does exist in *H. longicornis*, although there is never any damage to the contenders (Weygoldt 1972b). The fact that most individuals found in this study were alone in a given tree or log suggests that, at least during part of their lives, adults of *H. longicornis* are territorial and/or intolerant to conspecifics of the same sex. Moreover, the positive correlation between the size of the whip spiders and the DBH of the trees on which they were found suggests that large individuals can hold the largest trees, which present a higher probability of presenting buttresses.

The results on habitat use by *H. longicornis* have some implications for the conservation of this large whip spider in the Central Amazon. Since individuals prefer large trees, the anthropogenic disturbance promoted by selective logging or the degeneration of the forest structure due to fragmentation and edge effect may have a negative effect on *H. longicornis*. Indeed, Bloch & Weiss (2002) showed that the density of *P. longipes* was greater in plots assigned to areas with a moderate history of anthropogenic disturbance (> 80% of tree cover) than plots assigned to coffee plantations (50–80% of tree cover) or intensive logging (< 50% of tree cover). In a similar way, if the

density of *H. longicornis* is negatively effected by the lost of tree cover, we predict that the small fragments, in which large trees are virtually absent (Laurance et al. 2000), may function as sink habitats for the whip spiders and in many of these Amazonian fragments the species may be locally extinct.

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REGIONAL SEISMIC SONG DIFFERENCES IN SKY ISLAND POPULATIONS OF THE JUMPING SPIDER *HABRONATTUS PUGILLIS* GRISWOLD (ARANEAE, SALTICIDAE)

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ABSTRACT. Jumping spiders have long been used as model organisms to study visual communication. However, recent studies documenting the presence of intricate multicomponent seismic songs during courtship displays suggest an important role of seismic communication as well. Given the relatively recent focus on seismic communication, the extent to which seismic songs vary among jumping spider species or even among populations remains poorly understood. Here, we use the extensively studied *Habronattus pugillis* Griswold 1987 complex to explore putative seismic song diversity among males from isolated populations. *H. pugillis* populations have been studied extensively because of the tremendous diversification of male visual secondary sexual ornaments observed among adjacent mountain-top populations in southeastern Arizona ("sky islands"). Here, we aim to explore putative parallel patterns of diversification in seismic courtship songs between different sky island populations. Using laser vibrometry, we examined in detail the songs of three mountaintop populations (Atascosa (AT), Santa Rita (SR), and Santa Catalina (SC)) and observed an extraordinary diversity of songs and song types among these three populations. Large differences were seen in both the temporal and spectral properties of male seismic songs. In addition, we observed differences in song complexity between populations with some populations having "simple" songs (1 component) and others having "complex" songs (3 components). We also present preliminary data from four additional populations (Galiuro (GA), Huachuca (HU), Mule (MU), and Patagonia (PA)). Results from this study suggest that the diversification of male visual signals observed among populations of *H. pugillis* finds a counterpart in male seismic songs

Keywords: Seismic communication, signal evolution, species diversification, Salticidae

Jumping spiders have proven to be fruitful models in the study of ecology, behavior, and evolution, particularly as it relates to visually guided behaviors (Land 1969a, 1969b, 1985; Eakin & Brandenburger 1971; DeVoe 1975; Williams & McIntyre 1980; Blest et al. 1981; Land & Nilsson 2002). Studies have demonstrated the amazing visual abilities that jumping spiders possess by focusing on behaviors from a variety of contexts including predatory, navigational, mating, and competitive interactions (Crane 1949; Jackson 1977; Hill 1979; Forster 1982a,1982b; Richman 1982; Clark & Uetz 1990, 1992, 1993; Tarsitano & Jackson 1992, 1994, 1997; Edwards & Jackson 1994; Jackson & Pollard 1996; Harland et al. 1999; Harland & Jackson 2000, 2001, 2002; Nakamura & Yamashita 2000; Taylor et al. 2000, 2001; Clark & Morjan 2001; Jackson et al. 2005; Li & Lim 2005; Nelson et al. 2005; Hoefler & Jakob 2006; Nelson & Jackson 2006; Su & Li 2006). However, recent research has highlighted the utilization of seismic (vibratory) songs during courtship displays (Jackson 1977, 1982; Edwards 1981; Gwynne & Dadour 1985; Maddison & Stratton 1988a, 1988b; Noordam 2002; Elias et al.

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2003) and a few studies have demonstrated that these seismic songs are crucial for mating success (Elias et al. 2004, 2005, 2006a). Despite the recent increase in studies focused on seismic communication in jumping spiders, we still know very little about the taxonomic breadth and/or importance of this mode of communication within the family Salticidae.

Jumping spiders in the genus *Habronattus* have been the subject of extensive studies focused on species diversification, phylogeography, communication, mate choice, signal design, and sexual selection (Griswold 1987; Cutler 1988; Maddison & Stratton 1988a, 1988b; Masta 2000; Maddison & McMahon 2000; Masta & Maddison 2002; Elias et al. 2003, 2004, 2005, 2006a, 2006b; Maddison & Hedin 2003; Hebets & Maddison 2005). Not only is this genus diverse, with over 100 species described in North America (Griswold 1987; Maddison & Hedin 2003), but it also incorporates extensive morphological and behavioral differentiation among its many species. *Habronattus* males include some of the most elaborate male ornamentation and visual courtship behaviors known among any spider species (Peckham & Peckham 1889, 1890; Griswold 1987; Maddison & Hedin 2003). In addition to their elaborate ornamentation, it was recently demonstrated that some species of *Habronattus* produce complex multicomponent seismic songs (vibrations) simultaneous with visual signals during courtship (Maddison & Stratton 1988b; Elias et al. 2003, 2005, 2006a). Furthermore, these seismic signals were shown to be a crucial factor in mating decisions (Elias et al. 2004, 2005).

One particularly well studied group of *Habronattus* are those in the *H. pugillis* complex. In North America, populations of *H. pugillis* Griswold 1987 occur in woodland habitats isolated at the top of mountain ranges in southeastern Arizona and into Mexico. These mountain ranges are known as "sky islands" because their peaks form an archipelago of isolated woodlands separated by desert lowlands (Warshall 1995). Males from these various isolated populations are exceptional in that each possesses distinct secondary sexual traits involving both morphological and behavioral differences (Maddison & McMahon 2000; Elias et al. 2006b). While there is an impressive among-population variation in *H. pugillis* males, within a population or mountain range, males are very similar (Maddison & McMahon 2000). Using a combination of behavioral, molecular, and phylogenetic data, Masta & Maddison (2002) demonstrated that sexual selection was driving the observed diversification of male traits. Hebets & Maddison (2005) then suggested that a process of antagonistic co-evolution (Holland & Rice 1998) could be responsible for driving among-population variation in female mating preferences and associated male traits. In a reciprocal mate choice study, they found a xenophilic mating preference in which *H. pugillis* females from the Santa Rita Mountains preferred males from a foreign population, from the Atascosa Mountains, over their own local males (Hebets & Maddison 2005). Male *H. pugillis* from the Atascosa (AT) and Santa Rita (SR) populations were also recently observed to produce complex seismic songs (Elias et al. 2005, 2006a). In a follow-up study exploring the previously established SR female preference for AT males (Hebets & Maddison 2005), Elias et al. (2006a) demonstrated that a female bias for complex/novel seismic signals was responsible for the observed xenophilic preference and suggested that a general bias for complexity/novelty among females could have contributed to the rapid diversification observed in the *H. pugillis* group (Masta 2000; Masta & Maddison 2002).

The goal of this particular study was to document and compare seismic courtship songs of *H. pugillis* populations. In so doing, we demonstrate that the striking diversity of visual displays observed among populations of *H. pugillis* finds a counterpart in seismic songs among populations. We detected differences in both the temporal and spectral properties of songs between populations. In addition, we observed differences in the complexity of songs, with some populations having songs with a single component and others having multiple components. This is the first study to our knowledge to show regional differences in spider songs. We suggest that seismic songs along with visual ornaments are under strong selection in *H. pugillis* and we discuss the evolutionary forces that may have driven this diversification of seismic songs.

METHODS

Spiders.—Male and female *H. pugillis* were collected from different mountain ranges in Arizona (Atascosas (AT) 31°24.63′N, 111°8.77′W; Santa Ritas (SR) 31°40.38′N, 110°52.82′W; Santa Catalinas (SC), 32°21.40′N, 110°55.37′W; Galiuros (GA), 32°34.58′N, 110°16.50′W; Huachucas (HU) 31°25.94′N, 110°17.50′W; Patagonias (PA) 31°23.87′N, 110°44.44′W, and Mules (MU) 31°29.68′N, 109°59.82′W) over three field seasons (April–June 2002, April–May 2003, April–May 2004). Males and females were collected as immatures and adults. Male courtship songs were recorded up to a maximum of 3 mo after the animals were collected. As males senesce, they cease to initiate courtship and instead avoid or act aggressive towards females (Elias, pers. obs.), thus only males that actively courted females were used. Animals were housed individually in plastic containers (AMAC Plastic Products, Petaluma, CA; 3 × 3 × 5cm) and kept segregated by sex. Animals were kept in the lab on a 12:12 light: dark cycle. Spiders were fed fruit flies (*Drosophila melanogaster*) and juvenile crickets (*Acheta domesticus*) once a week. Male voucher specimens are deposited at the Royal Ontario Museum, Toronto, Canada.

Recording procedures and analysis.—Detailed measurements on seismic songs were made using laser vibrometry (Elias et al. 2003). We first anesthetized a mature female *H. pugillis* with CO_2 and tethered her to a wire with low melting point wax (beeswax). We held females in place with a micromanipulator on a substrate of nylon fabric (25 × 30 cm) stretched across a needlepoint frame to standardize the tension of the nylon. As courting substrate has significant effects on signal transmission (Magal et al. 2000; Cokl et al. 2004, 2005; Elias et al. 2004), we used the nylon fabric as our courting surface since it has negligible resonance characteristics and passes all frequencies equally (Elias et al. 2003, 2006c), thus enabling us to observe all the potential temporal and frequency components of a male's song. Mature males were dropped individually onto this substrate 15 cm from the female and allowed to court freely. Recordings began when males orientated towards females. Fifteen different females were used to initiate courtship from thirty-nine mature males. Males were collected as matures and thus we have no data on male age. We recorded seismic vibrations using a laser doppler vibrometer (LDV) (Polytec OFV 3001 controller, OFV 511 sensor head) (Michelsen et al. 1982). Pieces of reflective tape (approx. 1 mm^2) were attached to the underside of the courtship substrate 2 mm from the female to serve as measurement points for the LDV. The LDV signal was recorded on the audio track during standard video taping of courtship behavior (Sony DVCAM DSR-20 digital VCR, 48 kHz audio sampling rate). Spectrograms were made using Raven software (Cornell University, Lab of Ornithology). We present detailed measurements of spider songs of three populations (AT, n = 15; SR, n = 12; SC, n = 12). Means are given ± SD.

As it was not possible to record songs for all the populations using LDV, we present preliminary data on songs from four more populations (GA, n = 10; PA, n = 5; MU, n = 3; HU, n = 3) that we recorded using a custom piezoelectric sensor built from a turntable needle cartridge. For this recording technique, the courtship arena was a sheet of graph paper attached to a square cardboard frame (60 × 45 cm). Females were tethered as above and the male's seismic signals were recorded using a piezo-electric sensor placed directly underneath the tethered female. Ten different females were used in piezo-electric recordings. In comparing populations where we recorded a male's signal using both LDV and the piezoelectric sensor, we observed that although low frequency responses (<150 Hz) were relatively attenuated by the piezoelectric sensor, the male's signals were not significantly altered and all signal components were apparent albeit at lower amplitude (Elias et al. 2003). All piezo recordings were conducted in a sound-attenuated chamber at Cornell University. Seismic signals were amplified (Nikko NA790), recorded on the audio track of a video recording as above (48 kHz audio sampling rate) and high-pass filtered (> 150 Hz). We present examples of typical spider songs from the recordings available.

As all recordings were conducted with tethered females, it is possible that males behave differently under these conditions than they would in the field. These differences however appear to be more in the duration of courtship displays and not in the individual song components. For example, in situations where fe-

males were not tethered, males courted for longer durations overall, but used the same song components (Elias, pers. obs.). In addition, since males were collected as matures, they may have previously mated in the field. Here, also, we suggest that previous experience is unlikely to alter the specific components of seismic signal production but, instead, alters more plastic behaviors such as courtship duration or latency to court.

RESULTS

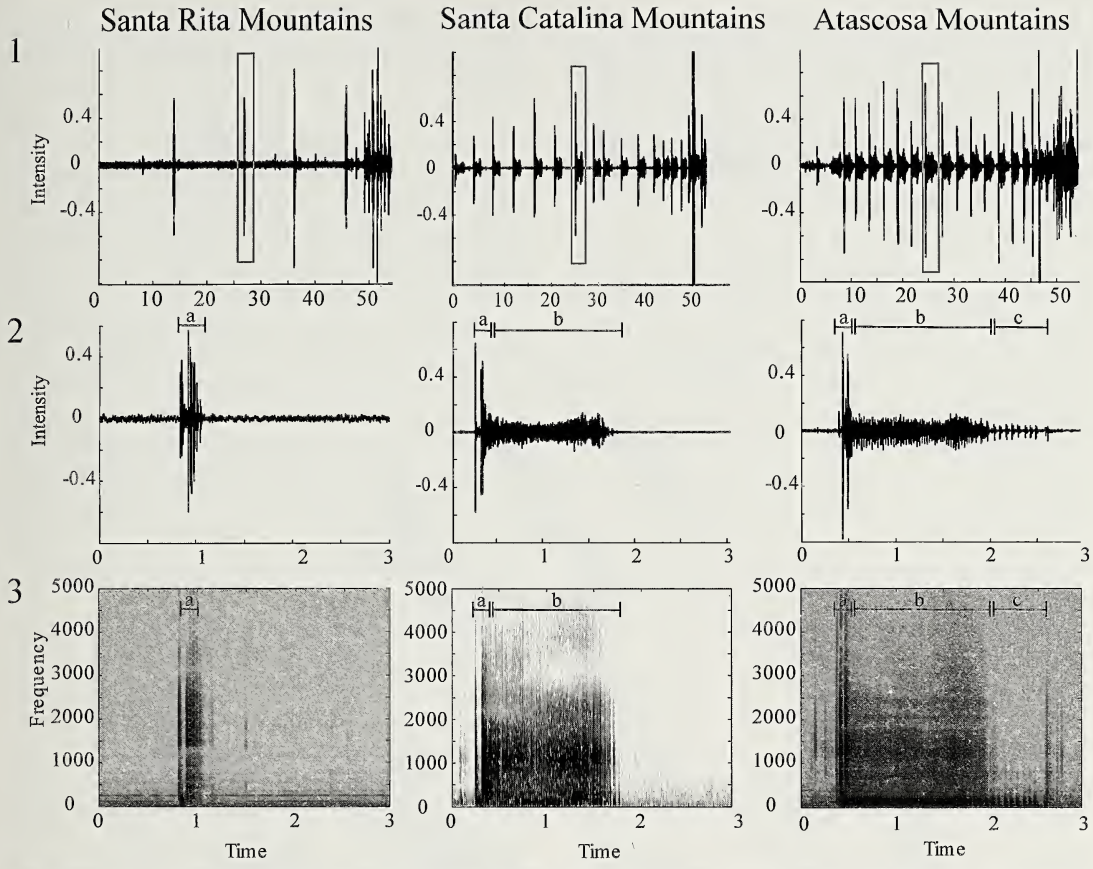
Visual courtship signals in *H. pugillis*.—The visual courtship behavior of *H. pugillis* varies by population, but in general courtship can be divided into two main stages: (1) the approach stage and (2) the pre-mount stage (Maddison & McMahon 2000). In the approach stage, the male raises and spreads his first pair of legs and lowers and spreads his palps. The male then proceeds to approach the female either directly or in a sidling motion while flicking (rapidly moving) his forelegs and pedipalps in a stereotyped manner. When the male gets within one to two body lengths of the female, the pre-mount stage begins (Maddison & McMahon 2000). In the pre-mount stage, the male's approach slows down, and leg and pedipalp flicking becomes more rapid—especially downward flicks of the first pair of legs. Males also scrape the abdomen repeatedly against the carapace just prior to mounting a female. It was suggested by Maddison & McMahon (2000) that this grinding corresponded to the production of seismic songs.

Seismic songs in *H. pugillis*.—Seismic songs are, in fact, produced by *H. pugillis* males at the moment the abdomen is seen to rub against the carapace. Preventing the abdomen from moving relative to the carapace prevents song production (Elias et al. 2006a). Song production varies from population to population and males can produce songs in the approach stage and/or the pre-mount stage. Song production is usually coordinated with flicking of forelegs. The general *H. pugillis* song can have three components. The first component (A) ("crackle") is generally of short duration, broad frequency and relatively high intensity; crackles have an impulse-like quality. The crackle component is generally the first song component produced and is present in all observed populations of *H. pugillis*. Some populations only include the crackle component (see below) and these tend to have crackles that are longer in duration than populations with additional components. The second component (B) ("rasp") is generally long in duration and broad in frequency. Rasps occur in all populations immediately prior to an attempted mount but, in some populations, from long distances. The third component (C) ("drone") is short in duration and broad in frequency but occurs at lower frequencies than crackles. Drones occur in bouts consisting of multiple signals produced rapidly following each other.

All *H. pugillis* songs are composed of similar song components, but there is variation in (1) the types and number of components and (2) the temporal and spectral characteristics of the different components. Below are detailed descriptions of male songs of three different sky island populations followed by preliminary descriptions of four additional populations.

Courtship behavior of *H. pugillis*.—*Santa Rita (SR) males:* The courtship behavior of SR males begins with rotations of the palps (Maddison & McMahon 2000). This palpal rotation is unique to SR males and is continued throughout the courtship display. Palpal rotations are often punctuated with rapid leg flicks. Males remain mostly stationary during courtship until the actual approach to the female, which is generally direct rather than sidling. The final stages of courtship involve the male holding his first pair of legs above the female and flicking the tips. Leg flicking occurs less often than in other populations (i.e., AT, SC, PA, HU). Leg flicks are coordinated with seismic songs (Fig. 1) which consist of a single component. SR seismic songs are of variable duration but are generally short (0.56 $\pm$ 0.393 s; n = 17) and consist of high intensity, broad band (range: 0–2850 Hz; peak frequency: 1082 $\pm$ 540 Hz; n = 17) crackles (labelled "a" in Fig. 1). Some SR males include rasps at extremely short ranges just prior to attempted copulation (Fig. 1, 48–55 s, SR column). The majority of seismic signals however only include the crackle component (Fig. 1).

Santa Catalina (SC) males: SC courtship begins with rapid foreleg flicks followed by body shakes (rapid side-to-side movements) during the approach stage of courtship (Mad-



Figures 1–3.—*Habronattus pugillis* song from the Santa Rita, Santa Catalina and Atascosa mountain populations. 1. Oscillograms of seismic songs. 2. Detail of oscillograms (boxes in Fig. 1). 3. Spectrogram of song in Fig. 2. The notation a–c in Figs. 2 & 3 identifies the three seismic components of male songs.

dison & McMahon 2000). After body shaking, males approach females with vigorous foreleg flicking. Seismic signals are produced during leg flicks preceding body shakes as well as during late display leg flicks. Seismic signals are not produced during a body shake bout but occur immediately after body shaking ends. Every foreleg flick is coordinated with a seismic signal (Fig. 2). SC male seismic songs are long in duration (1.30 ± 0.20 s; n = 15) and occur in two distinct parts (Fig. 2). The first part consists of a short (0.13 ± 0.16 s; n = 15), high intensity, broad band (range: 0–3937 Hz; peak frequency: 844 ± 349 Hz; n = 15) "crackle" (labelled "a" in Fig. 2). The second part consists of a prolonged long duration (1.17 ± 0.19 s; n = 15) broadband "rasp" (range 1: 7–1211 Hz; peak 1 frequency: 185 ± 198 Hz; range 2: 900–2500 Hz; peak 2 frequency: 1373 ± 317 Hz; n = 15) (labelled "b" in Fig. 2).

Atascosa (AT) males: AT locomotory courtship consists of rapid sidling, in which males move in large arcs alternating in direction with the first pair of legs held continuously above the ground (Maddison & McMahon 2000). After sidling, males approach females with vigorous foreleg flicking. Seismic signals are produced during leg flicking and not during the sidling display. Every leg flick is coordinated with a seismic signal (Fig. 3). AT male seismic songs are long in duration (1.85 ± 0.30 s; n = 15) and occur in three distinct parts (Fig. 3). The first part consists of a short (0.11 ± 0.03 s; n = 15), high intensity, broad band (range: 0–2640 Hz; peak frequency: 1069 ± 339 Hz; n = 15) "crackle" (labelled "a" in Fig. 3). The second part consists of a prolonged (1.07 ± 0.34 s; n = 15) broadband "rasp" (range 1: 0–650 Hz; peak 1 frequency: 203 ± 218 Hz; range 2: 530–2010 Hz; peak 2 frequency: 1170 ± 210 Hz; n = 15) ("b"

in Fig. 3). The third part consists of a variable number of "drones" (3–9; $n = 5$) of short duration (0.04 ± 0.01 s; $n = 18$) broad band (range: 0–1850 Hz; peak frequency 371 ± 457 Hz; $n = 18$) signals ("c" in Fig. 3). Broad band drones also occur along with rasps in the second courtship stage ("b" in Fig. 3) but are lower in intensity than rasps.

Other H. pugillis *males:* We observed the seismic songs of four additional populations, Galiuro (GA), Huachuca (HU), Patagonia (PA), and Mule (MU) mountains (Fig. 4). Detailed measurements were not available for these populations and we were only able to record songs using the piezoelectric device (see above). It is possible that we were not able to observe all song components using this method of sound recording therefore, future recordings will be conducted using LDV.

Galiuro (GA) visual courtship consists of a "first leg wavy circle" where the first legs are held forward and the tips moved in circles simultaneously (but out of phase) (Maddison & McMahon 2000). Periodically the first legs come into phase (sometimes punctuated with a rapid leg flick). Seismic songs are produced coincident with the first legs coming into phase (with and without leg flicks). Seismic songs in the GA population are made of crackles (a) and "slow" crackles (s-a) (Fig. 4). Slow crackles appear to consist of a series of crackles. Slow crackles have an impulse-like punctuated quality like crackles and are different from rasps as rasps are produced as a continuous signal.

Huachuca (HU), Mule (MU), and Patagonia (PA) male courtship songs are similar to SC male courtship with the notable absence of body shakes. HU, MU, and PA males approach females with flicking of the first pair of legs. Seismic songs are produced during leg flicks. HU, MU, and PA male seismic songs occur in two distinct parts, crackles ("a," Fig. 4) and rasps ("b," Fig. 4). In the early stages of courtship, HU males also add a unique component to their display. HU males approach females slowly with the forelegs held above the ground the entire time. Periodically males open and close their chelicerae during this approach. Seismic signals are produced intermittently as the male slowly approaches the female. Seismic signals during this portion of the display consist of crackle components and are not coordinated with any movement of the forelegs. This character is unique among all the populations studied (data not shown).

DISCUSSION

H. pugillis is undergoing diversification driven by sexual selection (Maddison & McMahon 2000; Masta 2000; Masta & Maddison 2002; Hebets & Maddison 2005; Elias et al. 2006a). Evidence suggests that sexual selection acting on male secondary sexual characteristics has driven extensive morphological and behavioral divergence between populations on the sky islands of south eastern Arizona (Maddison & McMahon 2000; Masta & Maddison 2002). Here we show that the diversity observed previously was only a partial picture and is further manifested in the evolution of distinct and stereotyped songs among different populations.

H. pugillis songs consist of similar components, although some populations have more complex songs than others. Males from the Santa Rita Mountains have simple songs, consisting of a single component. Males of the other populations have more complex songs with males from the Santa Catalinas having songs consisting of two components, and males from the Atascosas having songs consisting of three components. In addition to these broad scale differences between populations, temporal and spectral components are different between each population. There also appears to be variation in the coordination of visual and seismic components of courtship. Signal evolution involving seismic signals is thus potentially occurring along three axes: (1) frequency and temporal characteristics, (2) song complexity, as measured by the number of seismic components and, (3) multimodal coordination. Diversification in *H. pugillis* has probably occurred on a small temporal and spatial scale suggesting that the song differences between populations are likely due to selection and not random effects (Maddison & McMahon 2000; Masta 2000; Masta & Maddison 2002). Below we discuss some of the hypotheses that may drive the observed diversity of songs.

Spectral and temporal properties in animal songs often relay information about mate quality and/or species identity, resulting in substantial selection on song properties (Andersson 1994; Bradbury & Vehrencamp 1998;

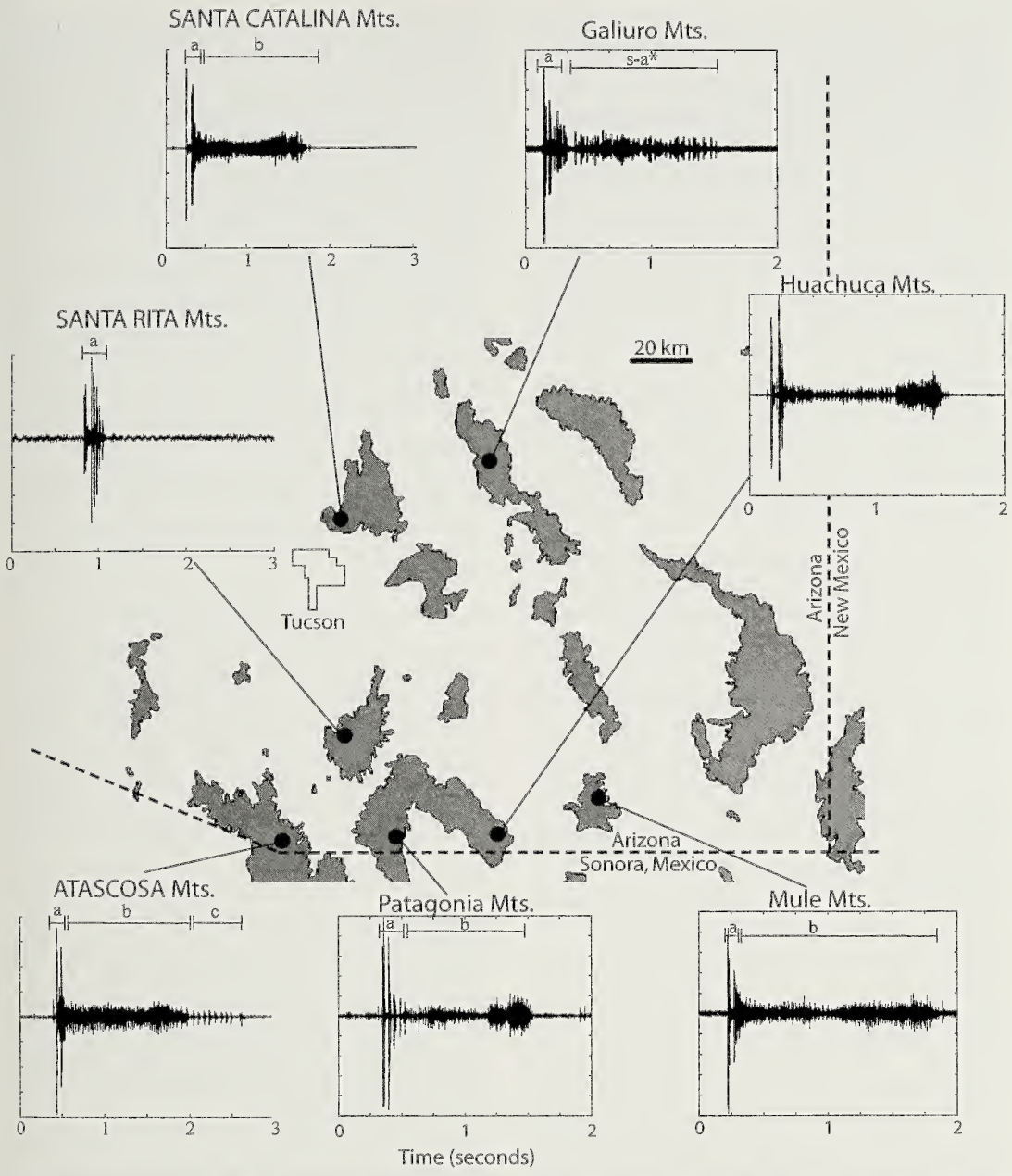


Figure 4.—Seismic song diversity in the sky islands of southern Arizona. Map of southern Arizona mountain ranges with outlines representing the lower limit of oak woodland habitat (Brown & Lowe 1982), corresponding to an elevation of ~1300–1500 m. Dots show collecting localities for *H. pugillis*. Representative songs are shown for populations recorded using laser vibrometry (all caps—Atascosa, Santa Rita, Santa Catalina Mts.) and a piezo-electric sensor (Galiuro, Mule, Patagonia, and Huachuca Mts.). a–c denote the three possible seismic components of male songs. *s-a denotes a "slow crackle".

Kotiaho et al. 1998; Parri et al. 2002; Gerhardt & Huber 2002). This may be the case in *Habronattus* songs as well (Elias et al. 2005). The characteristics of the signaling environment (e.g., leaves, sand) can also add substantial selective pressures on signal evolution and on the spectral and temporal characteristics of signals (Michelsen 1978; Larsen & Michelsen 1983; Romer 1998; Magal et al. 2000; Elias et al. 2004; Cokl et al. 2005). For example,

Elias et al. (2004) demonstrated that seismic songs in *H. dossenus* Griswold 1987 could propagate well on only a subset of available substrates, resulting in differential mating success for males across substrates. Elias et al. (2004) went on to suggest that evolution may lead to substrate specialization and a tuning of spectral and temporal signal characteristics to the particular signaling substrates available. Similar selective pressures may have lead to differences in the temporal and spectral properties of songs between different sky island populations.

There also appears to be variation in song complexity between sky island populations. Differences in song complexity among populations may be due to differences in the signaling environment between sky islands. Efficacy-based hypotheses of complex signal function such as the multiple sensory environments hypotheses (Candolin 2003; Hebets & Papaj 2005) suggest that multiple signals evolve when there is variation in the signaling environment so that under some conditions some signal components can be transmitted effectively when other signal components are not. Under an efficacy backup hypothesis (Hebets & Papaj 2005), one would predict the AT signaling environment to be the most variable, followed by the SC and the SR signaling environments. While this possibility remains to be explicitly tested, there are no obvious differences between sky island signaling environments (Masta & Maddison 2002).

Differences in song complexity between populations may also be due to selection for signal content, such as the need to convey multiple differential messages (Moller & Pomiankowski 1993; Johnstone 1996; for review of content-based hypotheses see Hebets & Papaj 2005). *H. pugillis* females mate only once (Hebets, unpublished observations), therefore informative signals may be at a premium. Due to differential natural selection pressure across mountaintop populations, it is possible that males from different populations might need to convey different aspects of quality to local females, resulting in divergent complex displays. Variable population densities could also influence complex signaling evolution as increased population density could increase male competition for mates, potentially resulting in an increase in display complexity as males are forced to provide information about multiple aspects of quality. The observed correlation between population density and signal complexity however is in the exact opposite direction, as our collection sites with the most spiders (SR) had the simplest seismic songs (Elias, Hebets & Maddison, unpubl. data). Clearly, future studies focused specifically on testing these hypotheses are necessary.

A role of antagonistic coevolution has been suggested in the evolution of complex, divergent courtship displays of *H. pugillis* (Hebets & Maddison 2005; Elias et al. 2006a). Under antagonistic coevolution models (Holland & Rice 1998), females are expected to evolve resistance to exploitative male signals thus forcing males to elaborate signals that are beyond the current realm of the female's resistance. Following from this, females are predicted to prefer males with novel exploitative traits over males with local traits for which they have evolved resistance. Under this scenario, if differences in song complexity in *H. pugillis* are being driven by antagonistic coevolution, then we would predict the following: SR females should prefer AT and SC songs over their own male songs (SR); SC females should prefer AT songs over SR songs and their own male songs (SC); and AT females should not show any preference. Hebets & Maddison (2005) have already demonstrated that SR females prefer AT males, and that AT females did not show any preferences between SR and AT males. In addition, Elias et al. (2006a) showed that SR females preferred AT males only if they could produce seismic signals. Results thus far are consistent with the hypothesis that differences in song complexity are being driven by antagonistic co-evolution.

If we include songs for which we only have preliminary data, there also appears to be variation between the coordination of visual and seismic signals. Some populations show no multimodal coordination in certain song components (HU population), while others show high degrees of coordination (AT, SC, MU populations). Coordinated signaling in multiple modalities can present animals with multiple advantages including reduced signaling costs (sender), reduced processing costs (receiver), and increased information content (Honey & Hall 1989; Partan & Marler 1999, 2005; Rowe 1999; Candolin 2003; Uetz &

Roberts 2002; Hebets & Papaj 2005). Differences in the importance of coordination and/or differences in the cross-modal interactions between visual and seismic signal could also lead to the differences observed between the different populations.

Although, we have only described a small proportion of *H. pugillis* songs, our results show an interesting parallel with regional song differences in birds (Krebs & Kroodsma 1980). Examining other sky islands in the US and Northern Mexico will likely reveal an even greater diversity of songs and song types. Given the extraordinary diversity of songs observed in this and other studies (Jackson 1977; Edwards 1981; Gwynne & Dadour 1985; Maddison & Stratton 1988a, 1988b; Noordam 2002; Elias et al. 2003, 2005), we propose that jumping spiders are a good system to study the function and evolution of songs.

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UNUSUALLY LONG *HYPTIOTES* (ARANEAE, ULOBORIDAE) SEQUENCE FOR SMALL SUBUNIT (18S) RIBOSOMAL RNA SUPPORTS SECONDARY STRUCTURE MODEL UTILITY IN SPIDERS

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ABSTRACT. We report on the structure of the small-subunit ribosomal RNA (18S rRNA) sequence from *Hyptiotes gertschi* (Araneae, Uloboridae), which is the largest 18S gene sequenced in any arachnid to date. We compare this remarkable sequence to those from a range of other spiders and arachnids, and develop base-pairing models of its insert regions to determine its overall secondary structure. The *H. gertschi* sequence of 1902 bases is 86 nucleotides longer than any comparable spider sequence and contains 5 inserts between 5 and 28 bases in length, all at regions characterized as among the most variable in eukaryotic 18S genes. Inserts were also found in one of these variable regions in published sequences of 3 species of hard ticks (Acari, Ixodidae). Other arachnid taxa were remarkably uniform in 18S primary sequence length, ranging from 1802 to 1816 nucleotides. Thermodynamic modeling of the *H. gertschi* inserts suggests they are largely self-complementary, extending the stem portions of the variable regions.

Keywords: Phylogenetics, arachnids, Acari, gene inserts

The small subunit ribosomal RNA, or 18S rRNA, is one of a small set of commonly used sequences for molecular phylogenetic reconstruction of arthropod relationships (reviewed in Caterino et al. 2000). The gene coding for the 18S rRNA contains sections that are highly conserved, and these provide informative characters for the assessment of relationships between distantly related taxa, such as metazoan relationships (Giribet & Wheeler 2001; Mallatt et al. 2004). The 18S rRNA has also been used in studies of divergence between arachnid orders, as well as studies of divergence between spider genera and species (Wheeler & Hayashi 1998; Arnedo et al. 2004). In the context of arachnid molecular phylogenetics, to understand both the potential utility and drawbacks in the use of any genetic marker, it is important to have knowledge of the amount of variation in both the primary sequence and secondary structures across taxa at different levels. This is because the secondary structure can influence the rate at which different parts of the primary sequence vary.

The genes coding for ribosomal RNAs contain regions that can accumulate and lose bases through insertion and deletion events (indels) more easily than protein-coding genes, which are constrained by the requirement that they maintain an open reading frame for proper translation into a functional primary amino acid sequence. Indels can change the length of the gene and make homology assessments of individual base-pairs, and often long stretches of base-pairs, difficult. The proper methodological approach to this sequence-alignment problem is a source of controversy in phylogenetics, and opinions range from using static alignments, with regions that are difficult to align being either included or discarded (e.g., Nardi et al. 2003); to using direct optimization (Wheeler 1996), which avoids the arbitrary removal of data and possible evolutionary signal and avoids the problem of multiple-sequence alignment altogether. An additional feature of direct optimization, as implemented in the program POY (Wheeler 1999) is the ability to treat inserts as multistate characters with as many states as there are unique insert

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sequences, with a matrix of character-state transformation costs. See Giribet & Wheeler (2001) for an example of implementation of the latter method.

A very different approach, and one that has been promoted by many authors, is the use of secondary structure models to aid in homology assessment and relative weighting (Dixon & Hillis 1993; Kjer 2004). Recently, it has been proposed that elements of rRNA secondary structure can provide a basis for choice between multiple models to be used in a partitioned Bayesian analysis (Telford et al. 2005). For this technique, bases from a variety of taxa would be compared to a secondary structure model for the gene for assignment to "stem" and "loop" (and possibly transitional or ambiguous) partitions. These partitions would be individually tested for the most appropriate likelihood models, then subsequently analyzed using the partitioned, multiple-model approach.

The RNAs produced by the 18S genes form secondary structure by base-pairing with their own complementary stretches of sequence, forming helical structures commonly referred to as stems, while the non-pairing regions form loop structures that connect multiple stems, or form the terminal turn in the self-complementary stems. Because the overall secondary structure is functionally important for the ribosome, and because two complementary changes in primary sequence are required to maintain a stem structure, it has been proposed that the stems should be treated differently in phylogenetic analysis than the less-constrained loops (Dixon & Hillis 1993). To do so requires the ability to tell whether nucleotides are in a loop or a stem structure, which can be modeled using computer algorithms that develop secondary structures based on comparative or thermodynamic information (reviewed in Gardner & Giegerich 2004).

Here we present a comparison of 18S structures sampled from arachnid orders and spider lineages to assess the utility of secondary structure information currently available for making homology judgments across arachnid taxa, and for determining data partitions used in model-based analyses. Included are new data from the species *Hyptiotes gertschi* Chamberlin & Ivie 1935 (Araneae, Uloboridae), and remarkably similar sequences from hard ticks (Acari, Ixodidae) that demonstrate the evolutionary conservation of the overall structure of the arachnid 18s gene.

METHODS

Taxon sampling.—We sampled exemplar sequences from all arachnid orders and major spider lineages for which at least one full sequence of the entire 18S gene was available in GenBank (http://www.ncbi.nlm.nih.gov/Genbank/). To sample unusually long arachnid 18S sequences thoroughly, we extended our search to include all "partial sequences" that came within 90 bases (~5% of the gene length) of the primer regions, since this region is highly conserved across arthropods and the missing length could be estimated despite lack of primary sequence. In taxa where 18S gene length was uniform and in the ~1800 base pair (= bp) length typical of arachnids, one individual was sampled, while all complete or nearly-complete sequences with large (> 3 bp) inserts relative to the *Aphonopelma* sp. sequence were included in the sample, since a complete secondary structure model is available for this taxon (Hendriks et al. 1988).

Among spiders, lineages included representatives from Mygalomorphae (*Aphonopelma sp.*, Theraphosidae), Mesothelae (*Liphistius bicoloripes*, Liphistiidae), Orbicularia (*H. gertschi*, Uloboridae), "derived orb-weavers" (*sensu* Coddington 1990), (*Nesticus cellulanus*, Nesticidae) and the RTA (retrolateral tibial apophysis) clade (*sensu* Coddington et al. 2004) (*Coelotes terrestris*, Amaurobiidae) (see Table 1). All spider sequences were from Genbank except for the *H. gertschi* data, for which new sequence data were generated in the current study. Specimens of *H. gertschi* were collected by S. Lew at the Angelo Reserve, Mendocino County (39°43′N, 123°39′W), and from Del Norte County near the Oregon border (41°59′N, 123°43′W), California, USA, in May 2003. Voucher specimens are stored in the collection of the Essig Museum of Entomology, UC Berkeley, under the voucher codes EMEC50654 and EMEC50993, respectively.

Molecular methods.—DNA was extracted from two legs from each of the *H. gertschi* specimens using a Qiagen DNeasy Tissue Kit's standard protocol. The 18S gene was directly PCR-amplified in three parts using primer pairs 1F-5R, 5F-9R, and 3F-7R (after

Table 1.—Taxa examined, with total gene length and p-distance between primary sequence of individuals and *Aphonopelma* sp. reference sequence. Length includes terminal primer regions (approximately 50 base pairs (= bp); 23 per primer + 4 bp downstream in the 3′ direction from primer 9R). * indicates partial sequences (see text), with lengths estimated by assuming uniform sequence length relative to reference sequence at missing terminal regions.

Order (lineage represented)	Taxon sampled	Genbank Accession Number	Total length (bp)	Uncorrected p-distance to reference
Araneae (Orbicularia)	*Hyptiotes gertschi* Chamberlin & Ivie 1935	DQ015708	1902	10.8%
Araneae (Mygalomorphae)	*Aphonopelma* sp.	X13457	1814	—
Araneae (Mesothelae)	*Liphistius bicoloripes* Ono 1988	AF007104	1808	2.4%
Araneae (derived orb-weavers)	*Nesticus cellulanus* (Clerck 1757)	AF005447	1816	7.8%
Araneae (RTA clade)	*Coelotes terrestris* (Wider 1834)	AJ007986	1814	5.7%
Opiliones	*Odiellus troguloides* (Lucas 1847)	X81441	1810	6.2%
Scorpiones	*Androctonus australis* (Linnaeus 1758)	X77908	1812	6.7%
Pseudoscorpiones	*Roncus* cf. *pugnax* (Navás 1918)	AF05443	1808	11.0%
Acari (Ixodidae)	*Amblyomma glauerti* Keirans, King & Sharrad, 1994	AF115372	1802	10.3%
Solifugae	*Eusimonia wunderlichi* Pieper 1977	U29492	1802	7.7%
Amblypygi	*Paraphrynus* sp.	AF005445	1810	4.8%
Uropygi	*Mastigoproctus giganteus* (Lucas 1835)	AF005446	1810	4.9%
Schizomida	*Stenochrus portoricensis* Chamberlin 1922	AF005444	1809	5.5%
Ricinulei	*Pseudocellus pearsei* (Chamberlin & Ivie 1938)	U91489	1813	5.1%
Palpigradi	*Eukoenenia* sp.	AF207648	1810	7.4%
Acari (Ixodidae)	*Sejus* sp.	AF287237	1880*	21.1%
Acari (Ixodidae)	*Lohmannia* sp.	AF287234	1887*	12.3%
Acari (Ixodidae)	*Alicorhagidia* sp.	AF022024	1872*	13.8%

Giribet et al. 1999), to amplify fragments of length ~950 bp, ~850 bp, and ~1000 bp, covering the first half, second half, and an overlapping central portion of the gene respectively. The PCR protocol (modified from Hedin & Maddison 2001) used 35 cycles of 30 s at 95° C melting temperature, followed by 30 s at an annealing temperature of 52° C, followed by an extension step of 45 s at 72° C, with 3 s added to this extension for every cycle after the first. In addition, these cycles were preceded by an initial melting at 95° C for 2 min, with a 7 min final extension at 72° C. A MasterAmp PCR Optimization Kit (Epicentre Technologies) was used to choose appropriate buffers to stabilize the PCR reaction, which improved yield and quality of PCR products. Molecular extraction vouchers were stored at −80° C.

Gene size, purity and concentration were assessed by running out a portion of the PCR product on a 1.5% TBE/agarose gel. PCR products were cleaned using Qiagen QiaQuick PCR Purification Kit, and cycle sequenced in both directions using dye terminators (after Sanger et. al 1977). Cycle sequencing products were analyzed using an ABI 3730 capillary autosequencing machine. Individual sequences checked against their complementary sequences, using Sequencher 3.1.1 (Gene

Codes Corporation). This program was also used to assemble contigs of all three overlapping primer regions for each *H. gertschi* specimen, to create a single sequence for each. Additional sequences (see Table 1 for accession numbers) were acquired from GenBank for comparison.

Alignment and Comparisons.—Using Clustal X version 1.83 (Chenna et al. 2003), a static alignment of multiple sequences was created using the default settings (gap insertion cost 15, gap extension cost 6.66, transition cost 0.5 times transversion cost). Treating the *Aphonopelma* sp. sequence and model as references, gaps in the aligned sequences were compared to the secondary structure model to detect regions where insertions and deletions have occurred.

Modeling of insert regions in *H. gertschi*.—In areas with insertions > 3 bp relative to the *Aphonopelma* sp. reference sequence, secondary structures were modeled using the web-interface version of the RNAfold program in the Vienna Package (http://www.tbi.univie.ac.at/~ivo/RNA/; Hofacker 2003). This program uses a dynamic-programming algorithm with a variety of parameters to estimate the secondary structure based on minimizing the free energy of the possible stem-loop structures from the primary sequence. The parameters used include RNA base-pairing energies plus a variety of experimentally determined adjustments to this cost, including energy estimates for loops of various sizes and locations, and for single- and double-stranded multi-base motifs known to affect local stability (Mathews et al. 1999).

The expanded regions of the *H. gertschi* 18S gene were modeled using the primary sequence of the insert region plus the four complementary bases at each insertion site that could be homologized with the reference sequence and structure from *Aphonopelma* sp. Because the RNAfold program had difficulty aligning the complementary 4-base-pair ends properly in some cases, we added a complementary 5-nucleotide extension at each terminus to anchor the ends of the sequence and stand in for the rest of the structure, so that each primary sequence input took the form: 5′-GGGGG- primary sequence -CCCCC-3′. We also tested the RNAfold program's ability to predict the structures in the variable arms of the Hendriks et al. (1988) *Aphonopelma* sp. model using the same method, then calculated the percentage of base-pairs and loop members in the algorithm output that correctly matched the model.

RESULTS

Comparisons of 18S sequence length and primary sequence divergence can be seen in Table 1. Most arachnid 18S sequences are in the range of 1800–1810 base pairs (including primer regions), with the *H. gertschi* and tick sequences being the exceptions (greater by 85 and 56–64 bases, respectively). Figure 1 shows a schematic of the Hendriks et. al (1988) model of spider 18S, with regions with *H. gertschi* and tick inserts marked with black arrows and a hatched bar, respectively.

***Hyptiotes gertschi* and tick insertions.**—The two *H. gertschi* sequences are identical, as are sequences from an additional set of amplifications of the Del Norte County specimen. However, in contrast to the marked similarity in length and structure across the arachnid exemplars from GenBank, the *H. gertschi* sequences are 86 nucleotides longer than the next-longest spider 18S (*Nesticus cellulanus*), and we estimate it to be 21 nucleotides longer than the next-longest arachnid 18S (*Sejus* sp., Acari, Ixodidae). This additional sequence is found in two large inserts—a 28-base extension of the helical arm E10-1 (Figure 2a), and 27-base extension of E10-2 (Fig. 2b)—and the rest is found as smaller inserts of 5, 6, and 13 nucleotides in helices 6, 41, and 47 respectively (Figs. 3a, b, and c). Three near-complete tick sequences were also found to have large inserts in the terminal arms of branch 10 (see Table 1).

Models of the *H. gertschi* inserts based on free-energy minimization show that the inserted sequences extend the helices in all of the cases except structure 6, where the helical stem is shortened and the terminal loop expanded. The RNAfold program also correctly replicated 90% (40 of 48) of the stem base-pairs in the Hendriks et al. (1988) model in the arms in which the inserts were found, which is comparable with the 73% base-pairing accuracy for this parameter set calculated by Mathews et al. (1999) using a variety of other well-characterized genes.

DISCUSSION

The most remarkable results from the current study were the number of sizable inser-

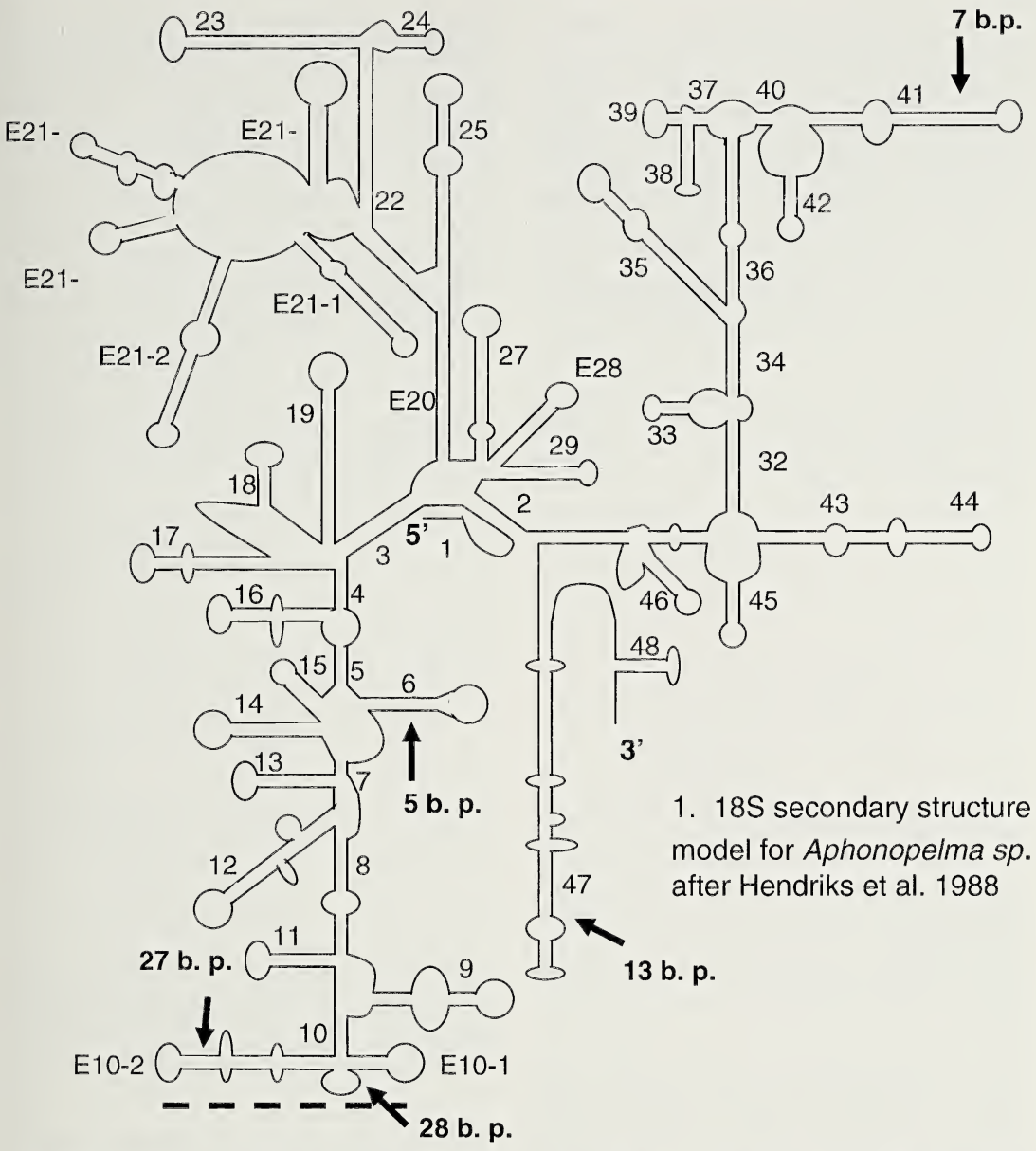
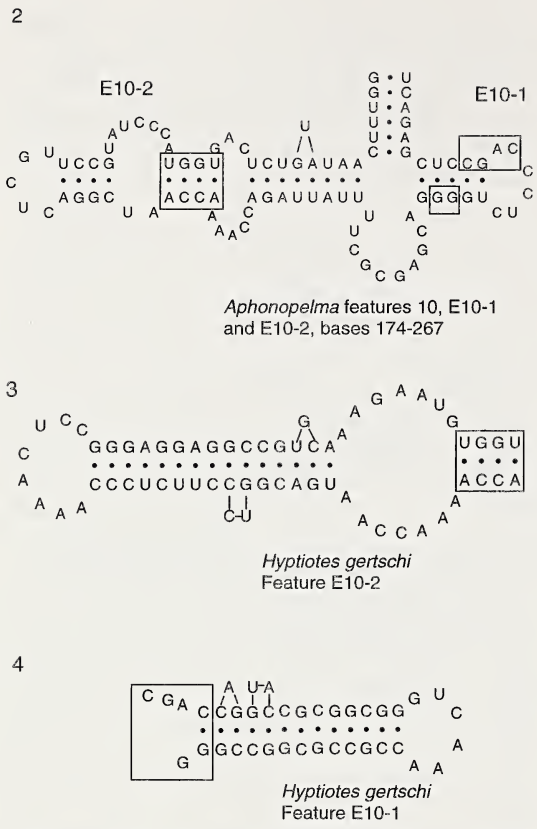
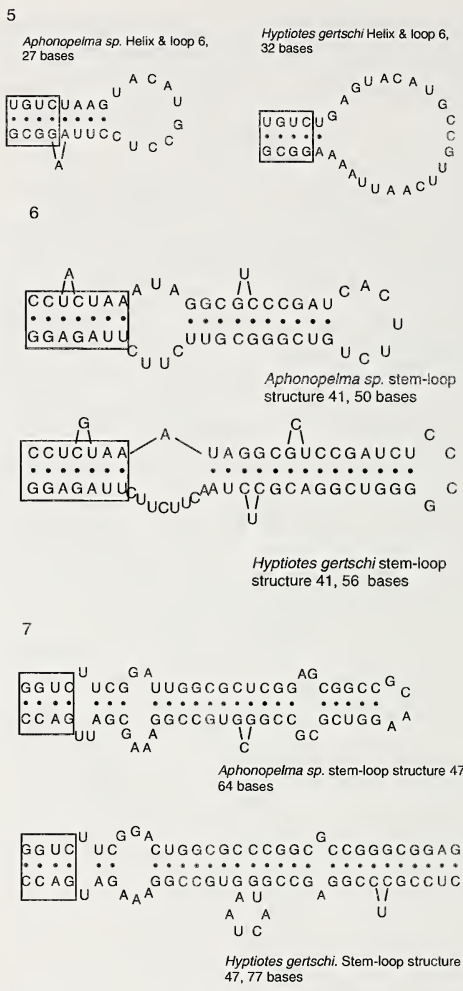


Figure 1.—General model for secondary structure of arachnid 18S ribosomal DNA. Small numbers refer to general stem-loop numbering system after (Nelles et al. 1984). Those features preceded by an "E" are specific to eukaryotic 18S sequences. Arrows and bold numbers refer to locations and size (in bases relative to tarantula model) of *H. gertschi* inserts, respectively. Hatched bar represents region with large inserts found in 3 tick taxa.

tions in the *H. gertschi* sequences and, in particular, the shared expansion of stem E10 found in both *H. gertschi* and ticks. In *H. gertschi* all insertions took place in known "variable regions" of the eukaryote 18S structure; helices 6, E10-1 and -2, 41, and 47 belong to regions that have been characterized as variable across a range of taxa (Van de Peer 1996). The RNAfold models show that much of the inserted *H. gertschi* sequence is self-complementary and these insertions function to extend the stem regions, rather than increase the loop size, except in Helix 6. This extension and maintenance of complementary



Figures 2–4.—Region of arachnid 18S gene with unusually large inserts. 2. Basic structure for helices 10, E10-1 and E10-2 in arachnids. Primary sequence and model after Hendriks et al. (1988); 3. Expanded E10-2 stem-loop structure in *H. gertschi*; 4. Expanded E10-1 stem loop in *H. gertschi*. Boxes represent areas of homology where expanded arms attach to conserved, adjacent parts of the structure.



Figures 5–7.—Smaller inserts and secondary structure model comparisons. 5. Structure 6 with 5 base pair insertion in *H. gertschi*; 6. Structure 41 with 6 inserted bases in *H. gertschi*; 7. Structure 47 with 13 inserted bases in *H. gertschi*.

stems has remarkable parallels with the findings of Hancock & Vogler (2000), who revealed a similar pattern of complementary stem expansion in the evolution of hypervariable regions of 18S in tiger beetles.

A variety of factors suggest the *H. gertschi* sequence represents the functional 18S rRNA gene rather than a pseudogene copy or experimental artifact. The presence of insertions in areas amplified by three different primer pairs, the replication of the sequence in individuals from two populations, the maintenance (and, in some cases, increase in length) of the base-pairing in stem structures, and the non-random, self-complementary sequence found in both large and small inserts, make it likely that we have sequenced a functional gene and not a pseudogene or an experimental artifact. One would expect to see decay of pseudogene sequence relative to the selectively-constrained functional gene (Giribet & Wheeler 2001), and this decay (in the form of random mutations) should be equally distributed throughout the sequence rather than restricted to known variable regions. Though some metazoans, such as helminths, are known to carry two functional copies of the 18S gene with differing sequences (Carranza et al. 1996), we found only single bands in our agarose gel visualizations of all three PCR products, and no second allele or double-peak patterns were seen in the raw sequence data,

despite repeating the amplification and sequencing processes, suggesting the existence of a single, uniform 18s sequence in *H. gertschi*.

How exceptional is the *H. gertschi* 18S rRNA? It seems to be an anomaly for spiders, which, based on those sampled in the current study, generally vary little even between the most distantly related lineages. Along with the tick data, these anomalous sequences show that the presence of large inserts in arachnids, though rare, is consistent with a general eukaryotic 18S evolutionary tendency—overall structure is maintained, while rare inserts appear in known variable areas. It is worth noting that only the *H. gertschi* gene contains expansions of several variable regions while the tick inserts are restricted to the E10 region.

With only two populations of *H. gertschi* sampled in the current study, we cannot establish the phylogenetic distribution of the 18S rDNA extension, whether it occurs in other *Hyptiotes* species, other uloborid genera, or their sister group, the Deinopidae. Such extensions have not been described from other Orbicularia, the sister-group of the deinopoid (Uloboridae + Deinopidae) clade, but may be more widespread within the deinopoids. The large number of inserts found in *H. gertschi* in this study suggests that there might be variation in number and size of inserts found in different taxa, since it seems unlikely that all these inserts appeared simultaneously. It would be interesting to map any such variation onto the existing phylogeny of Deinopoid genera (Coddington 1986) to determine the pattern of evolution of the 18S gene in greater detail. Alternatively, if variation seems to be limited to a subset of *Hyptiotes* or a small number of uloborid genera, the inserts themselves could be evaluated as phylogenetic characters within these groups.

Once the taxonomic range and amount of variation of these inserts has been characterized, hypotheses about causal biological, physiological or ecological factors allowing such inserts to occur can be tested rigorously. Comparative studies could also be performed with the wide range of metazoan taxa which show similar inserts, such as myriapods, proturans, and helminth worms, to find general correlations between 18S size and phenotypes (Carranza et al. 1996; Giribet & Wheeler 2001).

While the RNA folding algorithm used may not predict intra-molecular folding dynamics of rRNA accurately, it provides a repeatable method for producing a plausible structure for sequence data which lacks obvious homologs from related taxa for comparison. The algorithm also gives a reasonable basis for judging whether an insert extends a helix, a loop, or both, particularly with short sequences such as those modeled in this study. With changes affecting sequence length concentrated in the terminal ends of known stem-loop structures, the *H. gertschi* and tick 18S genes appear to be the exceptions that prove the rule; bases come and go, albeit very rarely, but the helical backbone and location of stem and loop structures of the small subunit ribosomal RNA have remained conserved throughout arachnid evolution.

Because the expanded sequence has only been found in a single spider species, it is impossible to argue that this is evidence of any trend in 18S evolution in spiders. However, the increase in size of the 18S gene seen here differs from the documented trend (relative to other metazoans) toward reduction in size in the hypervariable region of the mitochondrial 16S gene (Smith & Bond 2003) and in the arms of some tRNA genes (Masta & Boore 2004) of spiders. It should be noted that the cited trends are in mitochondrial genes, whereas 18S is part of the nuclear genome, and the two genomes may be subject to different selective pressures or constraints.

To understand the broader pattern of 18S size change, it is useful to look at the evolution of the 18S gene in other metazoan taxa. Giribet & Wheeler (2001) showed that the general pattern of 18S evolution across a much broader sampling of taxa, including hexapods, chelicerates, myriapods, and crustaceans, is one of conserved length in the 1800 bp range, with occasional increases in size. Deletion events appear to be exceedingly rare. The data presented here are in keeping with those findings, although the total length for the *H. gertschi* 18S gene is greater than that of any of the 49 chelicerate taxa reported by Giribet & Wheeler (2001) or of any full arachnid 18S sequence currently found in the Genbank database. Complete or nearly-complete sequences are required for secondary structure modeling since there is long-range complementary base-pairing in 18S secondary

structure (Telford et al. 2005). Unfortunately for the pursuit of whole-gene comparisons and structural modeling, many arachnid studies have used only half of the 18S gene, (e.g., Wheeler & Hayashi 1998; Arnedo et al. 2004), and there is a sizable and important spider lineage, the haplogynae, for which no complete 18S sequence is available.

As for the overall utility of 18S data for arachnid phylogeny, this data set shows that the Hendriks et al. (1988) model is sufficient for locating structural changes in the 18S gene for all known arachnid genotypes, though the value of modeling based solely on primary sequence using thermodynamic predictions on a single taxon is limited. In the majority of cases, alignment is trivial with a mean of less than 1% sequence length divergence between most taxa. This similarity in sequence-length across Araneae is also corroborated by data from a family-level study of the RTA clade by the authors (unpublished data). For data partitioning, relative-weighting, and model-choice purposes, the number and locations of the stem-loop structures of the 18S gene remain largely identical to that of most sequenced eukaryotes. Determination of stem and loop regions should be achievable with some confidence for the large majority of arachnid cases, using the Hendriks et al. (1988) model as a guide.

In exceptional situations where homology assessments or stem-loop status of individual bases are difficult, such as within the tick-specific inserts seen here, removing the insert data may be defensible, for two reasons: first, the tendency of insertions to occur independently in the same areas across widely divergent taxa (such as spiders and ticks having inserts in the E10 region) could plausibly add homoplasy to a data matrix and place taxa in incorrect groupings. Second, because the insertions tend to be small relative to the more easily homologized portions of the rRNA (much smaller, for instance, than the $>$ 200 bp insertions found in many myriapods, see Giribet & Wheeler 2001), and only occur in a small number of taxa, there is likely to be little reduction in phylogenetic signal from the sequence if an insert region is excluded from analysis.

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ANATOMY AND PHYSIOLOGY OF GIANT NEURONS IN THE ANTENNIFORM LEG OF THE AMBLYPYGID *PHRYNUS MARGINEMACULATUS*

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ABSTRACT. Amblypygids have modified front legs that are not used for locomotion, but rather to probe the environment in the manner of antennae. These elongate, motile sense organs are referred to as antenniform legs. We have found remarkable replication in structure and function of giant neurons in the antenniform leg of the amblypygid *Phrynus marginemaculatus* C. L. Koch 1841 when compared with other amblypygids. These neurons have such large diameter axons (several μm) that their action potentials can be recorded outside the cuticle. Their cell bodies are found in the periphery, in the distal-most segments of the antenniform leg, centimeters away from the central nervous system. Primary afferents from sense organs on the antenniform leg synapse onto some of the giant fibers in these distal segments of the leg. Standard histological techniques and a novel whole mount preparation were used to identify the location of giant cell bodies within the antenniform leg. We found several new cell bodies in segments 10–20, three of which were predicted by previous electrophysiological studies of another amblypygid, *Heterophrynus elaphus* Pocock 1903. Electrophysiology was used to show that the structure and function of four of the giant neurons, GN1, 2, 6, and 7, is very similar in *P. marginemaculatus* and *H. elaphus*. *Heterophrynus elaphus* inhabits humid tropical forests in South America while *P. marginemaculatus* individuals were collected from a pine rock hammock in the Florida Keys, USA. The similarity of findings in species with such distinct habitats suggests that the giant neurons are required for basic neuromechanical operation of these extended limbs, and are not subject to intense selection via ecological factors.

Keywords: Whip spider, giant neurons, mechanoreceptor, antennae

Giant neurons are a specialization of the nervous system in many animals that has enabled investigators to observe directly how neuron structure and function bring about behavior. Having exceptionally large diameter axons, giant neurons conduct action potentials very quickly (on the order of one to tens of meters per second). As conduction velocity scales with the square root of diameter, this increase in axon diameter and hence conduction velocity is one way in which organisms can reduce the conduction time of nervous signals. This results in faster turnaround from perceived stimuli to motor response. Selection pressure for fast escape behaviors is thought to have led to the development of the giant neurons found in squid, fish, crayfish, crickets, flies and cockroaches (Levine & Tracey 1973; Tauber & Camhi 1995; Mizrahi & Libersat 1997; Eaton et al. 2001; Jablonski & Strausfeld 2001). The function of the giant neurons in the above cases has been demonstrated clearly; their unusually rapid spike conduction time facilitates fast escape behavior.

Giant neurons and the conspicuous rapid behaviors they underlie have led to notable advancements in neuroscience. For example, in teleost fish, giant Mauthner neurons facilitate rapid evasive turning behavior. As a result, the entire neural pathway from sensory input (predator approach angle) to motor output (bilateral flexing of trunk muscles) is well understood and has been modeled mathematically (Eaton et al. 2001). Studies of wind-sensitive giant interneurons in the cricket are demonstrating how dendritic morphology produces complex spatiotemporal responses (Jacobs & Theunissen 2000). Finally, the painted redstart (*Myioborus pictus*) employs a visual display specialized to trigger giant neuron me-

diated escape responses, enabling them to forage more effectively (Jablonski & Strausfeld 2001). In all of these examples, giant neurons have served as a model system for understanding the neural system in general, at the anatomical, physiological, and behavioral levels, and have offered insight into the neural basis of behavioral and ecological adaptations.

Amblypygids (Arachnida, Amblypygi), commonly called whip spiders, have a system of giant neurons in their first pair of legs that, in addition to having unique morphology and synaptic connectivity, has not yet been linked to any behavior. Unlike most other arachnids, these nocturnal predators do not use this first pair of legs for locomotion. The legs instead are elongated, motile, sensory appendages that are used to probe the environment in a manner similar to insect antennae. The antenniform legs are very long relative to body size. At approximately 5 cm long for an adult *Phrynus marginemaculatus* C. L. Koch 1841, the antenniform legs are 5 times the width of the prosoma and 2.5 times longer than the walking legs, yet are very thin, measuring only 150 μm in diameter at the distal end. They are used in orientation, prey capture, agonistic displays, and even courtship displays (Weygoldt 1972, 1974; Beck & Gorke 1974; Foelix & Hebets 2001; Fowler-Finn & Hebets 2006). The tips of the antenniform legs are covered with various types of sensilla (Beck et al. 1974, 1977; Foelix et al. 1975; Igelmund 1987; Weygoldt 2000; Foelix & Hebets 2001), some of which have been shown (using electrophysiology) to have mechanosensory (Igelmund & Wendler 1991b) or olfactory (Hebets & Chapman 2000) function. Several other types of sensilla are also found on the antenniform leg tip, some of unknown function, and others that are morphologically similar to contact chemoreceptive or hygroreceptive sensilla, though this latter function has not been demonstrated with electrophysiology (Foelix et al. 1975; Beck et al. 1977; Foelix & Troyer 1980). The two nerves inside the antenniform leg contain some 20,000 small primary sensory axons (typically 100–200 nm in diameter) projecting from these sensilla, but they also contain several conspicuous giant neurons (axon diameter up to 12 μm).

Several features differentiate these giant neurons from those found in any other taxa. The cell bodies, or somata, of these giant neurons are found in the periphery, located in specific segments of the antenniform leg tarsus, in some cases centimeters away from the central nervous system (CNS). While some of these giant neurons are interneurons, others are proprioceptors. Synapses between primary afferent neurons and the giant interneurons also occur in the periphery, in the antenniform leg, a feature first discovered by Foelix (1975). Some of these synapses are axo-axonal, connecting the primary sensory neuron's axon to the *axon* of a giant interneuron. In almost all other arthropods studied to date, primary afferents project all the way into the CNS *before* synapsing onto second order neurons, making this peripheral integration a unique feature. Equally intriguing is the fact that the primary afferents, in addition to synapsing onto the giants, project in parallel all the way to the CNS. So the animal receives fast, highly summed information from the giant interneurons, and slower, sense organ specific sensory information in parallel. It is unknown whether primary afferents from olfactory or contact chemosensory sensilla synapse onto any of the giants, although stimulation with common odorants does not elicit spikes in the giants in another species of amblypygid, *Heterophrynus elaphus* Pocock 1903 (Igelmund & Wendler 1991a, b).

As intriguing as the morphological differences are, even more mysterious is the behavioral role of the amblypygid giant neuron system. The system does not seem to underlie escape or foraging behaviors. Touching the antenniform leg in a manner sufficient to elicit spikes in the mechanosensitive giants does not elicit an escape response of the animal, or even a reliable retraction of the antenniform leg (Igelmund & Wendler 1991b). In prey capture, touching a prey item with the antenniform leg does not directly precede the rapid strike movement, and often a delay of several seconds occurs between the touch and the strike (Foelix et al. 2002). Courtship and intraspecific aggressive behaviors are accompanied by high-speed (~30 Hz) flicking of the antenniform leg; whether they are mediated by the giant neurons remains to be seen (Weygoldt 2002; Fowler-Finn & Hebets 2006).

Although the majority of the 136 described species of amblypygid inhabit tropical and subtropical habitats, a few species are found in the temperate zones and still others inhabit

arid and semi-arid regions (Weygoldt 2000). With such a range of habitat types, one might expect environmental factors to play an important role in shaping the sensory biology of ecologically disparate species. The purpose of this study was to characterize the giant neuron system of *Phrynus marginemaculatus* and compare it with previously studied amblypygids, in an attempt to shed light on the behavioral role of these giant fibers. The specific question that drove this study was whether these giant neurons are broadly used tools, supporting a variety of functions, or whether they are more specialized, facilitating species-specific tasks. Prior to this study, only the giant neurons in *H. elaphus* had been studied in detail using both histology and electrophysiology (Igelmund 1984, 1987; Igelmund & Wendler 1991a, b). Our studies suggest that while there are some similarities and differences between species, the giant neurons appear to remain conserved across disparate ecological niches.

We chose to study *P. marginemaculatus* for several reasons. While it is in the same family as *H. elaphus* (Phrynidae), the species used for earlier neurophysiological work, the two genera do not appear closely related (Weygoldt 1996). *P. marginemaculatus* is also the species about which we know the most. It has been the subject of several behavioral studies including those focusing on life cycle and development (Weygoldt 1970), reproductive behavior (Weygoldt 1969, 1974), male-male contests, and female-female contests (Weygoldt 1969; Fowler-Finn & Hebets 2006). Furthermore, the habitats of *H. elaphus* and *P. marginemaculatus* differ greatly. *H. elaphus* is found on the vertical surfaces of large buttressed trees underneath the dense tropical forest canopies of South America. Their habitat is extremely heterogeneous both in terms of physical structure and biotic composition. In contrast, *P. marginemaculatus* is found horizontally underneath limestone rocks in the relatively open pine rock hammocks of the Florida Keys, USA where the complexity of both physical and biotic structure is likely much lower. Comparing the giant neuron structure and function between *P. marginemaculatus* and the previously studied *H. elaphus* not only adds to our knowledge of the unique structure of amblypygid giant neurons, but also provides insights in the behavioral role of this giant neuron system.

METHODS

Specimens.—Adult male and female whip spiders (*Phrynus marginemaculatus*) were collected from Big Pine Key, Florida (24.67N, 81.35W) on 6–9 November 2002 and were brought back to the laboratory where they were housed and cared for in an identical manner to a previous study (Hebets & Chapman 2000). Voucher specimens are available from the personal collection of E. Hebets.

The antenniform leg of *P. marginemaculatus* comprises a femur (~1 cm long), tibia (~1.7 cm long), and tarsus (~2 cm long), resulting in an appendage ~ 5 cm in length (relative to a body length of 1 cm). The tibia and tarsus are made up of many cylindrical smaller segments, called pseudosegments, giving rise to visible segmental boundaries and repeated sensory structures, and having length on the order of roughly 0.5–1 mm. In keeping with past convention, the pseudosegments of the antenniform leg are labeled with increasing numbers starting at the distal-most tip. The tip segment then is 1 (segment is sometimes abbreviated S, hence the tip segment is S1), moving proximally with increasing number to the most proximal segment of the tarsus, at the tarsus-tibia joint, which was typically segment 59 (S59).

Histology.—Standard histological protocols were used to stain and image cross- and longitudinal sections of the antenniform leg. Three techniques were used. The first consisted of Propidium Iodide staining of whole mount preparations (Duch et al. 2000). The antenniform leg was clipped distal to the patella, and dissected in Schneider's culture medium at room temperature (RT). A sliver of razor blade was used to shave approximately the top third of the cuticle from the distal-most 30 segments of the tarsus. Tissue was fixed in 3.5% paraformaldehyde in PBS (phosphate buffered saline), and rinsed in several changes of PBS for 30 min. In two preparations, the tissue was incubated in RNase A (Sigma, 0.1 mg/ml, in PBS) for 30 min at 37° C, to reduce background staining. After being rinsed for 30 min in PBST (PBS + 0.3% Triton-X 100), the tissue was incubated in Propidium Iodide (Sigma, 1:1000 in PBST) for 60 min at RT. After final rinses in PBS, the

tissue was mounted on a slide with Vecta-Shield mounting media (VectaLabs, Inc.).

Methylene blue and Osmium Tetroxide stains were utilized with resin (Ultra Low Viscosity Embedding Kit, Polysciences, Inc.) embedded tissue. For both, the antenniform leg was cut into short (2–5 mm) tubes and fixed with an aldehyde based fixative. Osmium Tetroxide staining proceeded as documented in Igelmund & Wendler 1991a. Tissue was cut into 5, 8, and 10 μm thick sections using a Leitz 1512 microtome. Tissue that had not been stained with OsO_4 was stained on the slide with 1% methylene blue solution, before being mounted with Entellan mounting media. Slides were imaged with a Leica DM4000B compound microscope and DFC480 digital camera.

Propidium iodide staining of whole mount preparations provided adequate contrast to image the large cell bodies, was the most rapid imaging technique, and had the advantage of leaving long intact lengths of leg, which made noting in which segment each cell body was found an easy task. Due to the need to conserve our limited number of specimens for the electrophysiological studies, we discontinued our histological studies upon obtaining images adequate to resolve the axons within the nerve cross section and the locations of giant cell bodies.

Electrophysiology.—Extracellular recordings from the antenniform leg were made using a technique similar to that of Igelmund & Wendler (1991a). Animals were anesthetized with CO_2 or by placing them on a bed of ice for 3 min. Once anesthetized, they were restrained using strips of dental wax, and covered with a moist Kim-wipe to prevent desiccation. The antenniform leg was extended laterally and woven through four pairs of metal pins. These were made by cutting one side of a 16-pin DIP socket into four small plastic pieces, each containing two pins spaced by 2.54 mm. Electrochemical connection between each pin and the leg was made using a small amount of EEG paste. These pins constituted four pairs of differential recording electrodes, with the spacing between each pair being approximately 5 mm, that were connected to the positive and negative inputs of a differential voltage amplifier. As the distalmost 50 segments of the tarsus that we were interested in typically measured between 1 and 1.5 cm, we placed the electrodes as close together as possible. The amplifier was a custom built, miniature 16 channel extracellular voltage amplifier, with a gain of 1000. The 4 amplified signals were digitized (20 kHz sample rate) by a 16 channel FireWire A/D box (DAQPad, National Instruments, Inc.), and acquired directly into MATLAB (Mathworks, Inc.) for analysis.

Multichannel spike waveforms were analyzed in MATLAB using custom scripts that performed an amalgam of the most popular manual and automated sorting techniques (Lewicki 1998; Spence et al. 2003). Briefly, the raw waveforms were bandpass filtered (passband: 300Hz to 5 kHz), occurrences of spikes were detected and sorted by amplitude using an energy window filter, and then the distributions of propagation times between channels were used to identify unique spike types. The cleanest (i.e., not overlapping with other spikes on any other channel) individual spikes were extracted from the raw recordings, aligned on channel four, and averaged to produce a spike template (for details, see Spence et al. 2003). Each of these "templates" for a particular multichannel spike having distinct spike amplitude on each channel and distinct propagation time between channels is assumed to originate from an individual giant fiber.

Stimuli were applied manually under a dissecting microscope. For mechanosensory stimuli, a small plastic rod was used to gently deflect bristle hairs at various points along the antenniform leg. Two bouts of 30 sec of stimulation were applied at each point. For deflection stimuli, the same rod was used to deflect the antenniform leg laterally in the plane of the animal.

RESULTS

External morphology.—Ten molted, preserved, or whole mount antenniform legs were qualitatively surveyed with an optical microscope for the presence and distribution of sensilla. Examination confirmed the presence of bristle, club, porous and rod hair sensilla in addition to modified tarsal claws, a pit organ, and a plate organ (Igelmund 1987). The leaf-like hairs reported on *H. elaphus* were not systematically found, with a single leaf-like hair being found on only one animal out of 10 observed. The rod sensilla are grouped in a sin-

gle oval shaped patch on segment 1. The plate organ was typically found on segment 11, once on segment 13, and in one case two plate organs appeared: one each on segments 11 and 13. A bulbous (and angled relative to the plane perpendicular to the leg axis) segmental boundary appears at the S22/S23 boundary, as opposed to the S21/22 boundary in *H. elaphus*. This boundary likely contains the large slit sensilla reported for the similar boundary in *H. elaphus*, but we were unable to resolve the slit in the optical microscope.

Histology.—The internal morphology of the antenniform leg of *P. marginemaculatus* is similar to that of *H. elaphus*. At segment 40, the antenniform leg is approximately 140 μm in diameter (Figs. 1–3). Visible within the tarsus are 2 tendons, the lumen, a blood vessel and 2 large nerves. The nerves contain several large axons, the most readily apparent of which are 2 giant axons located in nerve 1, and 5 others in nerve 2 (Figs. 2, 3). These are in addition to an estimated 20,000–30,000 primary sensory afferents of much smaller diameter, of order 0.1 μm, contained in fascicles (Foelix & Troyer 1980). In this segment (40), the largest seven axons have effective radii (= r_{eff}) of 1.8, 2.1, 2.3, 2.5, 2.6, 5.1, and 6.8 μm respectively, where the effective radius is computed from

$$r_{eff} = \sqrt{\frac{A}{\pi}}$$

and "A" is the measured cross-sectional area of the axon (n = 1).

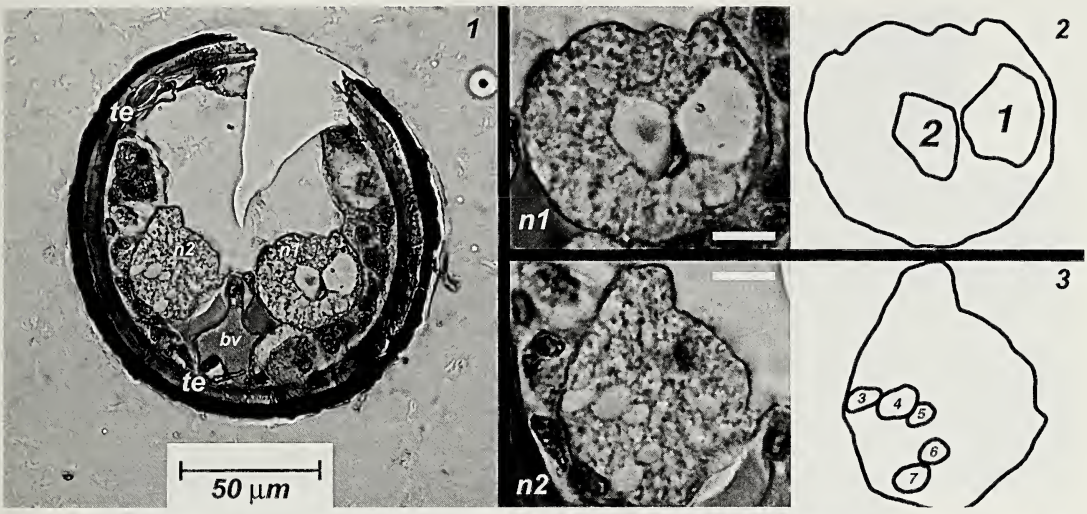
Longitudinal sections of the antenniform leg revealed giant cell bodies in segments 5, 6, 10, 11, 12, 14, 15, 16, 20, 22, 23, and 26 (Figs. 4–10). These somata are several tens of μm in length and width (the largest was in segment 6, measuring ~100 by 50 μm, Fig. 4), and are readily identified by their large size and distinct structure. They consist of an oval shaped outer cell body, a circular, outlined nucleus with homogenous, lightly stained interior, and an innermost nucleolus, which appears as a spot. The Propidium iodide stained cell bodies (Figs. 4–7) display a white outlined nucleus with dark interior, and the nucleolus appears as a white spot. The Osmium Tetroxide (Fig. 4) and Methylene Blue (Figs. 7, 10) stained cell bodies have the reverse contrast. It is assumed that these cell bodies give rise to the giant axons seen in Figs. 1–3.

The cell bodies in segments 11 and 26 were of slightly smaller size, having narrower and more elongated cell bodies, but still displaying the distinct circular nucleus and nucleolus (Figures 4–10). Finding the location of the cell bodies within the antenniform leg is useful because these results can be compared with multi-site electrophysiological recordings, establishing a connection between the observed cytology and sensory physiology.

Electrophysiology.—Large (~50 μV–1.5 mV) action potentials of varied amplitude and conduction velocity were recorded across 4 positions on the antenniform leg tarsus (Fig. 11). The spacing between pins in an individual recording pair was 2.54 mm, and the spacing between pairs was approximately 5 mm (see Fig. 11). For the purposes of understanding spike timing and conduction velocity, the spike can be thought of as "at" the midpoint between a pair of recording sites at the time when the inner part of its spike waveform crosses zero. Spontaneous activity from smaller units was common, while mechanical stimulation (brushing hairs or bending the leg) was required to elicit bursts of spikes from larger units. At least 7 distinct types of spikes were observed. Four of these were elicited repeatedly and classified reproducibly (n = 5 different animals) using mechanosensory stimulation. Stimulation of the bristle hairs at 3 different points along the tarsus (Fig. 11) was adequate to identify spikes corresponding to two of the giant neurons, which we label GN1 and GN2 following the convention of Igelmund & Wendler (1991a).

The largest spike, corresponding to GN1, had peak-to-peak amplitude 1.3 mV at segment 52 (recording site 4), and an average conduction velocity of 2.9 m/s. It responded to deflections of bristle hairs, maximally at the tarsus tip and with reduced sensitivity as the stimulation site was moved proximally (Fig. 11). The GN1 spike is generated at the site of stimulation, and propagates both proximally and distally inside the neuron, appearing on our most distal recording site at segment 10. GN1 is most likely the largest axon (Figs. 1–3, Axon 1), and one of the cell bodies in segment 5 or 6 (Fig. 4), due to its large spike amplitude and appearance on our segment 10 recording site.

The same bristle hair stimulation traces were also adequate to identify spikes origi-



Figures 1–3. Figure 1.—Cross section of the tarsus of the antenniform leg, stained with methylene blue. Labeled are two tendons (te), a blood vessel (bv), and the two nerves (n1 and n2). Enlarged views of nerves n1 and n2 are seen at right (Figures 2, 3), with outlines of the nerve bundle and largest seven giant axons. Scale bars in Figures 2 and 3 are 10 μm.

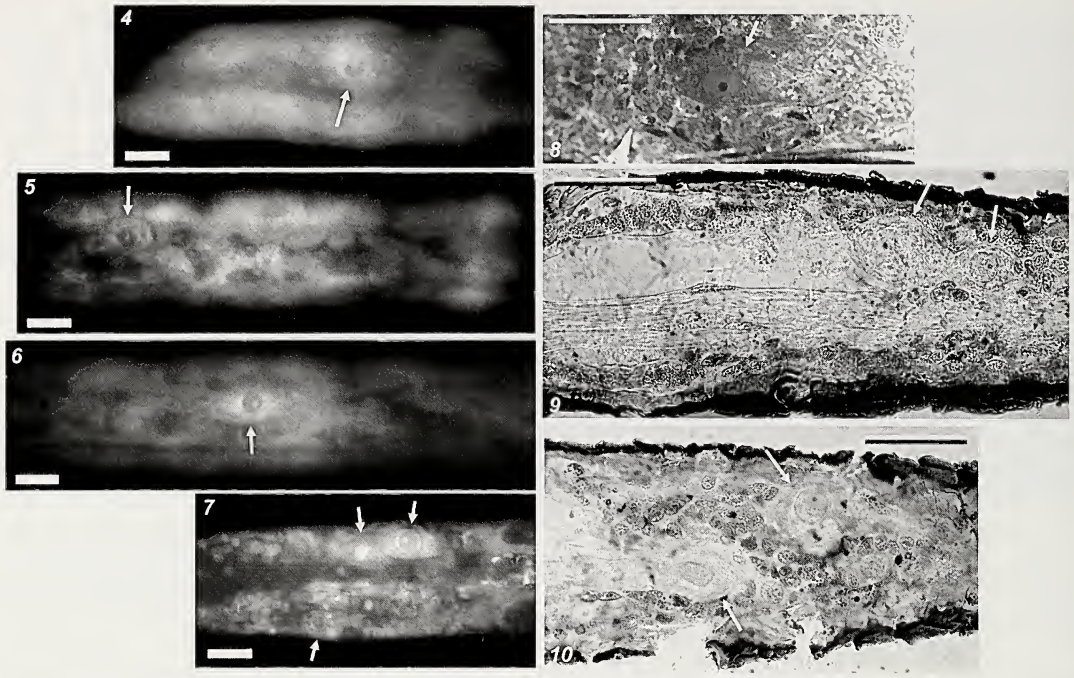
nating from GN2. Although this neuron's spike also originates at the point of stimulation and propagates in both directions, it is smaller in amplitude and conduction velocity than GN1 (0.41 mV and 2.6 m/s), and does not appear on our segment 10 recording site (Fig. 11). This places its cell body between segments 10 and 28. These traits suggest that it is GN2, and based on the similarity of our results to those of Igelmund & Wendler (1991a), it seems likely that it consists of one of the axons of intermediate size (Figs. 1–3, Axons 2–7), and one of the cell bodies found in segment 23 (Figs. 9, 10). The amplitudes and conduction velocities of both GN1 and GN2 we have found are similar to those found in *H. elaphus* (Igelmund 1984). The firing rates of GN1 and GN2 adapted quickly, with repeated stimulation of the same bristle hairs producing few spikes.

Two types of spike that responded to deflection of the antenniform leg near segment 20 were identified. Deflection (bending) of the tarsus at other points produced fewer or no spikes from these neurons. We did not localize the exact segmental boundary for which bending maximally elicits these spikes. The fact that these spikes responded to bending of the tarsus, propagated solely proximally, and did not appear on our segment 12 recording site (suggesting the cell body is proximal to segment 12 but distal to segment 28) identifies them as GN6 and 7. These spikes had relatively small average amplitude and conduction velocity (GN6: 0.20 mV and 1.8 m/s, GN7: 0.16 mV and 1.7 m/s). The amplitude of these spikes is in good agreement with that found for them in *H. elaphus*, which varied between 0.1 and 0.2 mV (Igelmund 1984).

DISCUSSION

Morphology of the antenniform leg of *P. marginemaculatus*.—We found that *P. marginemaculatus* has a close replication of the sensory physiology found in *H. elaphus*. The tarsus of the antenniform leg is equipped with similar classes of sensory organs, and with similar distribution. The rod hairs are grouped in a single oval-shaped patch on the first tarsal segment, which is similar to *H. elaphus*, but in contrast to *H. longicornis* Butler 1873, in which they are grouped in 3 distinct circular patches on each of the first 3 segments (Igelmund 1987). We did not repeatedly find the leaf-like hairs found on specific segments of *H. elaphus* (Igelmund 1987). In this manner, *P. marginemaculatus* is similar to *H. longicornis* and *H. batesii* Butler 1873, which also lack the leaf-like hairs (Igelmund 1987).

Internally, the antenniform leg of *P. marginemaculatus* has a neural architecture that closely parallels previously studied amblypy-



Figures 4–10.—Representative longitudinal sections of the antenniform leg. Whole mount Propidium iodide stains of the following segments: (Figure 4) 6 , (Figure 5) 10, (Figure 6) 12, and (Figure 7) 22, respectively. Osmium tetroxide stain of segment 10 (Figure 8, different specimen from Figure 5), and methylene blue stained sections of segment 23 (Figures 9 and 10). Single cell bodies (arrows) are visible in segments 6 (Figure 4), 10 (Figures 5 and 8), and 12 (Figure 6). Three are seen in segment 22 (Figure 7), and 23 (Figures 9 and 10; these are serial sections through the same tissue; two cell bodies are seen in Figure 9, and a third appears in Figure 10). Cell bodies (cf. panel Figure 4) consist of outer cell body membrane (in this case ~100 μm wide by 50 μm tall), inner nucleus (white circular line enclosing dark area, here 26 μm diameter) and innermost nucleolus (inner white spot, 6 μm diameter). Scale bars = 50 μm.

gids. The giant axons in *P. marginemaculatus* are distributed between the two nerves with remarkable similarity to *H. elaphus*. The largest 2 axons, presumably GN1 and GN2, are situated adjacent to each other in one nerve, while the remaining smaller axons are bundled together in the other nerve. The peripheral giant cell bodies and sensory synapses found in whip spiders (Amblypygi), whip scorpions (Uropygi), and harvestmen (Opiliones) are rare, and to date this type of neural architecture has only been found in a few cases within the animal kingdom (Foelix 1975; Foelix & Troyer 1980). Insects and other arthropods are thought to have their neuronal cell bodies and the first site of synaptic integration located centrally, either in the brain or ganglia.

We used a new preparation and staining method to image the giant cell bodies: whole mount dissection of the antenniform leg followed by Propidium Iodide labeling (Figs. 4–7). We found that the unique cytology of the giant neuron somata, especially the homogeneous, light staining inside the nucleus but outside the nucleolus, was reproduced with the Propidium Iodide stain (Figs. 4–7). This peculiar staining and large nucleus size led previous investigators to ask whether these cells were polyploid, but a Feulgen stain established that this was unlikely (Foelix & Troyer 1980). This new preparation provided a more rapid technique to locate in which segment each cell body lies, and resulted in longer, multi-segment pieces of intact antenniform leg for observation. This more readily enables observation of structures that span multiple segments, such as nerves, tendons, and blood vessels.

Giant cell bodies in segments 10–20, and

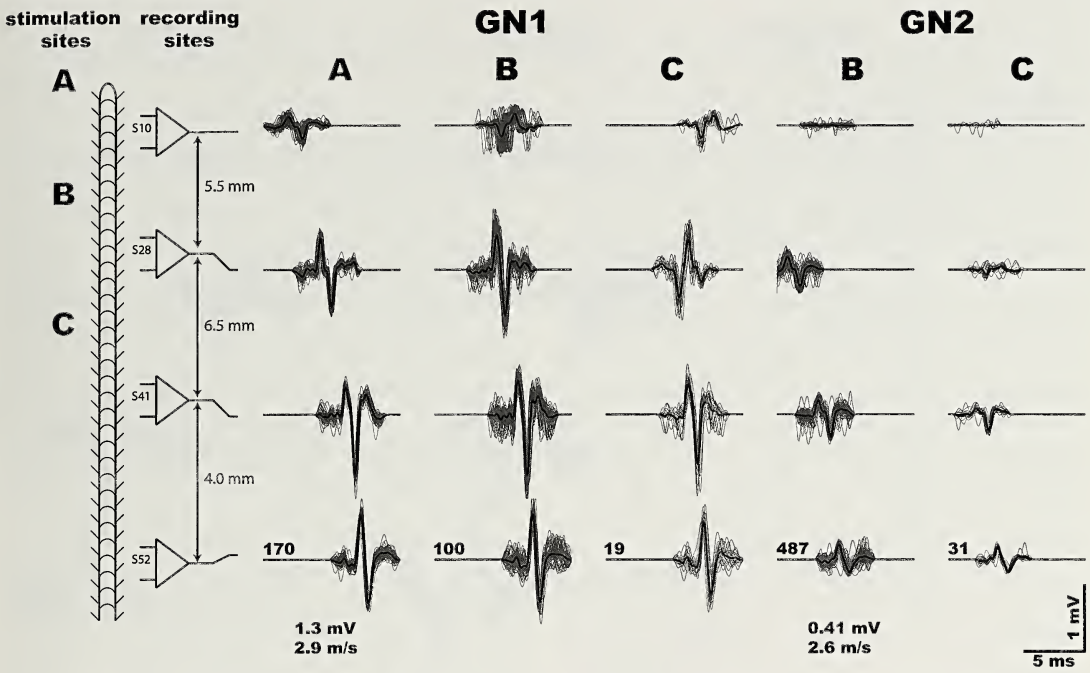


Figure 11.—Four point recording from the tarsus, and spikes from GN1 and GN2. Average spike (dark line) overlaid on individual spikes (gray lines). The number of individual spikes averaged to calculate each template is shown on the fourth recording site waveform. Peak-to-peak amplitude of average waveform on fourth site, and average conduction velocity are shown below the first GN1 and GN2 spike types. Propagation direction can be seen in time course between channels and as a reversal of peak order (proximal = positive then negative, distal = negative then positive). Spikes were aligned in time on the fourth recording site, and thus the variation in conduction time is most easily seen in the "jitter" of spikes on channel 1. The geometry of the recording pins is not drawn to scale. Separation between pins within a recording site is 2.54 mm, and the center to center spacing between pairs was approximately 5 mm. As a result the spacing between pins on the edge of neighboring pairs was also approximately 2.5 mm. The measured center to center spacings for this recording are indicated with arrows.

GN3, 4 and 5.—In *P. marginemaculatus* we have found giant cell bodies in segments 5, 6, 10, 11, 12, 14, 15, 16, 20, 22, 23, and 26. In *H. longicornis*, *H. batesii*, and *H. elaphus* giant cell bodies were found most frequently in segments 1, 5, 6, 13, 19, 20, 21, 22, 25 and 101 (Foelix & Troyer 1980; Igelmund & Wendler 1991a; Foelix & Hebets 2001). There is remarkable replication in the location of the cell bodies, with those in S5 and 6 being in the identical segment, and those in the region of 19–26 likely to be slightly shifted but homologous cell bodies. We found several new giant cell bodies between segments 10 and 20. This finding agrees with the electrophysiological results of Igelmund & Wendler (1991a), whose recordings predicted that the cell bodies of GN3, 4 and 5 would lie in this region. Now that the segmental location of these giant neuron cell bodies is known, tracer-fills of sensory neurons on individual segments can be pursued to look for connectivity between the giant neurons and the various sensilla. In addition to bristles, these sensilla include the club and porous hairs that are found on the distalmost ~20 segments, which are thought to have hygrometric and olfactory function, respectively. This is in addition to the slit sense organs that are found on each tarsal segment, which may sense cuticular stress or segmental deflection.

The sensory function of GN3, 4, and 5 is unknown. Although we recorded additional types of spikes that matched examples from these neurons in *H. elaphus* (Igelmund & Wendler 1991a), we could not elicit their activity with basic mechanosensory or odor stimuli. The odor stimuli used were a leaf-

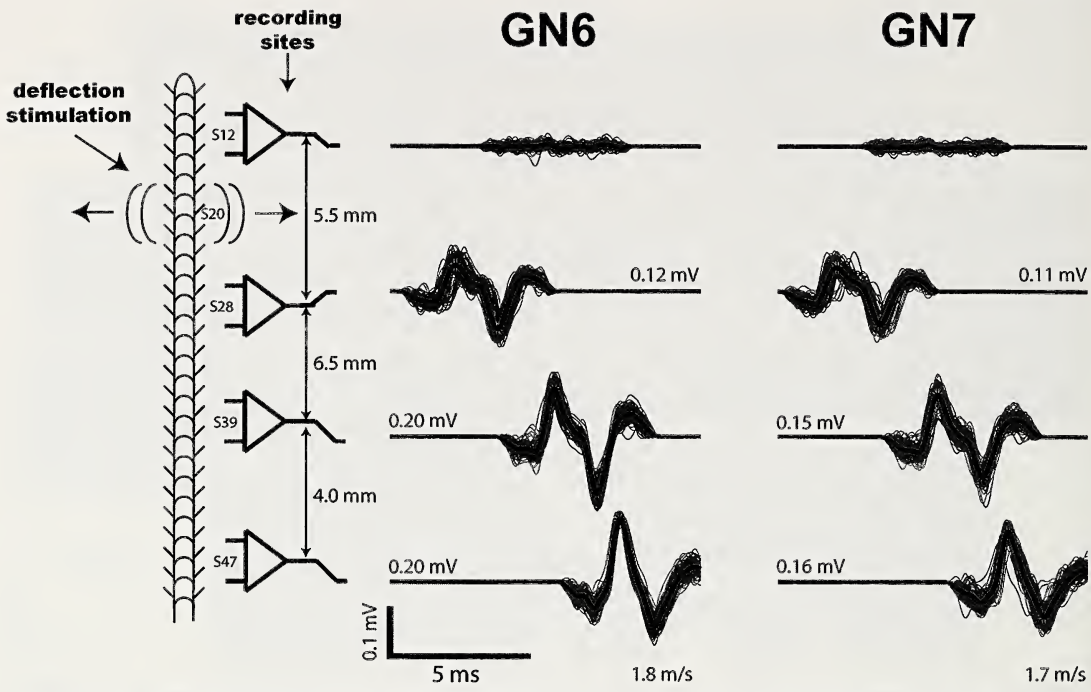


Figure 12.—Four point recording from the tarsus, and spikes from GN6 and GN7. Average peak to peak amplitudes are shown for each recording site, and the average conduction velocity denoted below. Both templates are averages of 100 individual spikes.

alcohol and a leaf-aldehyde, odorants commonly emitted by plants. This confirms some of the results for *H. elaphus*, in which mechanical, olfactory, and even temperature and hygrometric stimuli did not elicit a response from these neurons, apart from a phasic response of GN5 to tobacco smoke (Igelmund & Wendler 1991a).

Structure and function of giant neurons 1, 2, 6 and 7.—GN1 and GN2 are mechanosensory interneurons that respond to deflections of the bristle hairs. We were able to identify them clearly in *P. marginemaculatus* using several factors: their spike amplitude and conduction velocity, response to bristle hair stimulation, spike initiation at the point of stimulation and propagation in both directions, and the location of their cell bodies implied by the recording sites (i.e. GN1 distal to segment 10, GN2 between segments 10 and 28). We qualitatively tested the receptive fields of GN1 and GN2 in *P. marginemaculatus* and found agreement with *H. elaphus*: stimulation at the tip of the antenniform leg produces only GN1 spikes, stimulation at segment 20 produces both GN1 and GN2 spikes, and nearing segment 45 only GN2 spikes are elicited. Thus it appears *P. marginemaculatus* has a similar organization of GN1 and 2: GN1 covers the distalmost 20 segments, ramping down its sensitivity moving proximally as GN2 begins to take over, becoming more sensitive as segment 40 is approached. GN1 and 2 adapt quickly to repeated stimulation of the same bristles. Given their large (several mm) receptive fields and rapid adaptation, GN1 and 2 appear to function as rapid touch detectors for the tarsus.

GN6 and 7 are sensory neurons. They function as rapid proprioceptors, giving the animal feedback in the amount and direction of bending at the segment 22/23 joint. We were able to identify GN6 and 7 in *P. marginemaculatus* using similar criteria: their smaller amplitude spikes always originated at the same point (between segments 12 and 28), propagated solely proximally, and responded to deflection of the leg, all of which matches the behavior previously found in *H. elaphus*. GN6 and 7 are thought to be either coupled to a large slit sense organ at the segment 22/23 border, or part of a separate joint receptor mechanism at

that boundary. Either connectivity could allow them to perform their observed proprioceptive function.

Comparing histology with multi-site electrophysiology, it was found that in *H. elaphus* the GN1 cell body is the one found in segment 5, GN2 is in segment 23, and GN6 and 7 are two of four found in segment 22. Our electrophysiological results suggest that *P. marginemaculatus* has markedly similar structure and function of GN1, 2, 6, and 7. GN1 is one of the cell bodies in segment 5 or 6, GN2 is most likely in segment 23, and GN6 and 7 are two of those found in segment 22.

The role of the giant neurons in natural behavior.—The role of the giant fiber system of amblypygids in the natural behavior of the animal remains a mystery. Although there are cases in which giant fibers are not directly linked to specific behaviors (DiCaprio 2003), typically, in other arthropods, giant neurons facilitate rapid escape or predatory behavior (Levine & Tracey 1973; Tauber & Camhi 1995; Mizrahi & Libersat 1997). Touching the antenniform leg in a manner that elicits spikes in GN1 or 2, even repeatedly, does not evoke a rapid escape response of the amblypygid, while puffs of air directed at trichobothria on the walking legs usually does. Giant neurons can underlie rapid predatory behaviors (Gronenberg 1995a, b), but while amblypygids make rapid prey strikes with their pedipalps, the antenniform legs do not touch the prey immediately before a strike, and often a period of seconds will elapse between the last touch of the antenniform leg and the strike (pers. obs.).

Rapid tapping and vibratory movements are made with the antenniform legs during courtship and intraspecific aggressive behaviors (Weygoldt 2000; Fowler-Finn & Hebets 2006). High speed video of aggressive behaviors (Fowler-Finn & Hebets 2006) has found the frequency of tapping to be ~30 Hz. Spikes from GN1 take on the order of 30 ms to get to the CNS, and so it is possible that the animal could use GN1 to receive feedback during each cycle of the tapping behavior. While feedback at the same rate as the tapping may not be needed to regulate the behavior, it would be required in order to react to changes within a single cycle. Spikes in the primary afferents could not provide feedback on the time scale of a single tapping cycle: applying local circuit theory to these unmyelinated axons, we predict conduction velocity to scale as the square root of axon radius (Aidley 1998), and so estimate that primary afferents having a radius 20 times smaller than the giants would take ~140 ms to arrive at the CNS. This would give a maximum feedback driven tapping rate of about 7 Hz. However, the rapid adaptation of GN1 to stimulation of the same bristles, and the lack of an obvious need for feedback, makes this hypothesis (that GN1 exists to provide fast feedback for rapid vibrations) unlikely. It is possible that some of the other motor or proprioceptive giants facilitate this high-speed tapping of the antenniform legs. As the vibratory tapping occurs during courtship and aggressive behaviors, it seems likely that it signals individual quality, and is used as a basis of assessment of a mate or competitor. Whether information about quality is contained in the frequency of the vibration or some other component of the signal remains open. If the frequency of antenniform leg vibration were to signal the quality of an individual, however, this could be a source of evolutionary pressure on the development of a faster sensorimotor system in the antenniform leg.

Amblypygids will intermittently exhibit rapid retraction of the antenniform leg when touched, a behavior that appears highly dependent on the animal's state of alertness (Spence pers. obs.). Given the costs of losing these appendages (animals missing both legs cannot orient or proactively hunt), and perhaps even the costs of being entrapped by them, fast touch detection and rapid proprioceptive feedback may simply be required for adequate maneuverability in such long appendages.

The sense organs and underlying giant fiber system we have studied in *P. marginemaculatus* is remarkably similar to that of *H. elaphus*, yet the habitats of these two species, the Florida Keys for *P. marginemaculatus* and Brazilian rainforest for *H. elaphus*, are quite different. One predicts that the environment of *P. marginemaculatus* would offer a smaller diversity of prey, fewer vertical surfaces, more seasonality, a lack of canopy and correspondingly more light, and lower humidity than the Brazilian home of *H. elaphus*. The similarity in the giant neuron systems across these species suggest that they are crucial for the mo-

tility and basic function of the antenniform legs, and as such are not under great selection pressure from these ecological differences.

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A NEW SPECIES OF *PACHYCHERNES* (PSEUDOSCORPIONES, CHERNETIDAE) FROM MÉXICO ASSOCIATED WITH NESTS OF *NEOTOMA MICROPUS* (RODENTIA, MURIDAE)

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ABSTRACT. The new species *Pachychernes tamaulipensis* is described from all free-living stages collected in nests of the packrat, *Neotoma micropus*, in Tamaulipas, México. This species is related to *P. shelfordi*, *P. zehorum*, *P. attenuatus* and *P. baileyi*; all of them form a coherent group. The distribution of the pseudoscorpions in the different components of the nests is analyzed.

Resumen. Se describe la nueva especie *Pachychernes tamaulipensis* considerando todos sus estadios de desarrollo, los cuales fueron colectados en nidos de *Neotoma micropus* en Tamaulipas, México. Esta especie está relacionada *P. shelfordi*, *P. zehorum*, *P. attenuatus* y *P. baileyi*, los cuales forman un grupo coherente. Se analiza la distribución de los pseudoescorpiones en los diferentes componentes del nido.

Keywords: Taxonomy, morphology, Central America, ontogenetic series, packrat

Mammal and bird nests are microhabitats that provide favorable conditions for the development of a wide variety of arthropods (Beier 1948; Muchmore 1971). These include pseudoscorpions, which often occupy the nests of small mammals, especially of the order Rodentia, including various rats and mice in North and Central America (*Rattus norvegicus*, *Microtus* spp., *Dipodomys spectabilis*, *D. ordii*, *Mus musculus*, *Neotoma* spp., and *Perognathus flavus*), squirrels (*Spermophilus beecheyi*), gophers (*Thomomys monticola*), porcupines (*Erethizon dorsatum*) and beavers (*Castor canadensis*) (Chamberlin 1952; Hoff 1948, 1956; Hoff & Clawson 1952; Muchmore 1971). Twenty-one species of pseudoscorpions, belonging to 14 genera and eight different families are known to be associated with nests packrats (or wood rat) of the genus *Neotoma* (Villegas-Guzman 2003; Francke & Villegas-Guzman 2006).

The nests generally consist of four components. These are: the cover, formed by all those materials that protect the nests, like sticks of different sizes, prickly pear pads and other plant remains; the feeding chamber, where the pack rat stores its food, the nest proper, made of fine straw and where the rodent spends its periods of inactivity; and the passage-ways, which it uses to move between the nest components and the exterior (Álvarez et al. 1988).

Nine pseudoscorpion species belonging to the genus *Pachychernes* Beier 1932 are known (Harvey 1991; Muchmore 1990a, 1997); four of these form a coherent group (Muchmore 1997), and three have been found in Mexico: *P. shelfordi* Hoff 1946 from Mexico (without precise locality) and also found in Florida (Muchmore 1990b); *P. attenuatus* Muchmore 1990a from Yucatan and Quintana Roo and *P. zehorum* Muchmore 1997 from Chiapas. This group is characterized by the distinctive spermathecae of the females and the highly modified setae on the first legs of males, the latter representing an undoubtedly synapormorphic feature. The objective of this contribution is to describe another Mexican

member of this group, which was found in the nests of *Neotoma micropus* Baird in Tamaulipas.

METHODS

Five nests were dismantled carefully, with each component being placed separately in a plastic bag, labeled, and then transported to the laboratory, where they were processed using Berlese funnels and preserved in 70% alcohol. The pseudoscorpions were then prepared using Hoff's (1949) technique, modified following Wirth & Marston (1968).

We found 23 specimens: three females, one male, eleven tritonymphs, five deutonymphs and three protonymphs. These differ from the previously known species and are therefore described here as new.

Measurements are given in millimeters and were obtained using Chamberlin's (1931) method, as modified by Benedict & Malcolm (1977). They are reported in the text as means ± standard deviation; minimum and maximum values are given in parenthesis (only one measurement is given where no variation was observed). Abbreviations used in the description are: L = length, W = width, L/W = ratio length/width. Size comparisons with other species are based on the original descriptions.

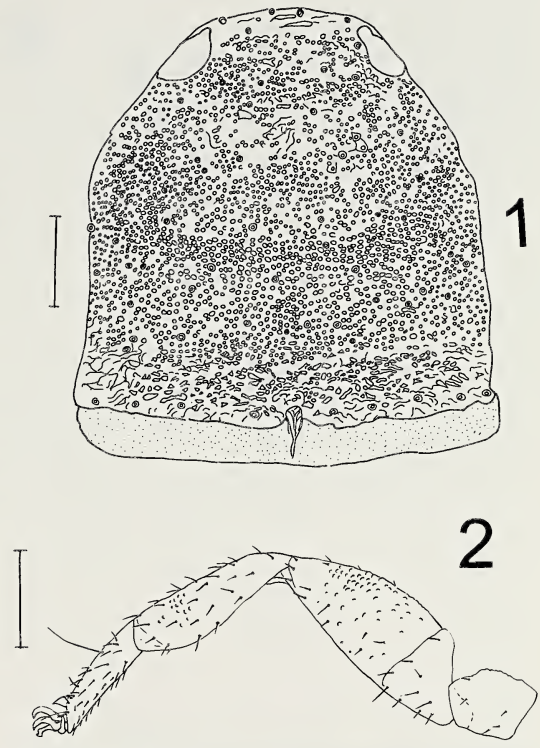
The types and other material examined are deposited in the Colección Nacional de Arácnidos (CNAN) of the Instituto de Biología, Universidad Nacional Autónoma de México and Colección de Artrópodos Asociados a Mamíferos Silvestres de México (CAAMSM), of the Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional.

TAXONOMY

Family Chernetidae Menge 1855
Genus *Pachychernes* Beier 1932

Type species.—*Chelifer* (*? Atemnus*) *subrobustus* Balzan 1892 by original designation.

Remarks.—The genus *Pachychernes* currently contains nine species: *P. subrobustus* (Balzan 1892), *P. baileyi* Feio 1945, *P. gracilis* (Ellingsen 1902), *P. robustus* (Balzan 1888), *P. subgracilis* (With 1908) and *P. subrobustus* (Balzan 1892) from South America; and *P. attenuatus* Muchmore 1991, *P. shelfordi* Hoff 1946 and *P. zehorum* Muchmore 1997 from Central America. A further species, *P. effossus* Schawaller 1980, was named from Oligocene Amber deposits from the Dominican Republic (Schawaller 1980).



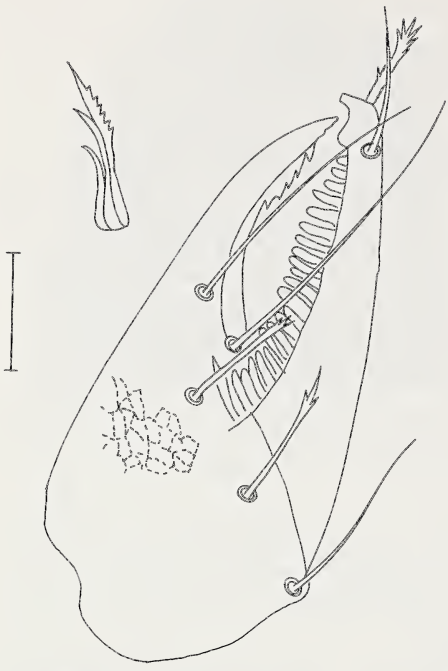
Figures 1–2.—*Pachychernes tamaulipensis*. 1. Female carapace; 2. Male leg IV. Scale lines: 1 = 0.2 mm; 2 = 0.3 mm.

Pachychernes tamaulipensis new species
(Figs. 1–10)

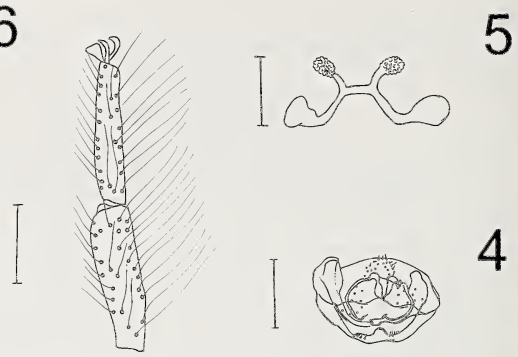
Type material.—MÉXICO: *Tamaulipas:* Female holotype (CNANT-0185) collected in nest of *Neotoma micropus* at 28.9 km N, 26.6 km E. of Soto La Marina (24°02′13.2″N, 99°56′49.2″W), 5 November 2001, G.A. Villegas-Guzman (CNAN). Paratypes: 1 male (CNANT-0186), 1 female (CNANT-0187) deposited in CNAN, 1 female (CAAMS-PS001), 7 tritonymph, 2 deutonymph, and 1 protonymph, with same data as holotype (CNAN).

Etymology.—The specific epithet refers to the place where the nests were collected, the state of Tamaulipas, and the fact that this is the first species of *Pachychernes* described for that state.

Diagnosis.—Carapace rectangular with 2 elongate eye-spots, with 1 poorly defined transverse furrow. Posterior margin very pale,



Figures 3–6.—*Pachychernes tamaulipensis*. 3. Female chelicera and flagellum; 4. Male genitalia; 5. Female spermatheca; 6. Male leg I. Scale lines: 3 = 0.05 mm; 4, 5 and 6 = 0.2 mm.



Figures 3–6.—Continued.

weakly sclerotized and with minute triangular scale-like markings. Chelicera: hand with 5 setae, *sb* and *b* denticulate, flagellum with three blades and serrula exterior with 24 plates. Spermatheca H-shaped with 4 lobes. Tarsi III/IV with an elongate tactile seta. Male: tibia and tarsus of leg I with a series of long thin hairs. The pedipalpal femur and carapace length of *Pachychernes tamaulipensis* are shorter than in *P. baileyi*, *P. attenuatus* and *P. zehorum*, but are slightly longer than in *P. shelfordi*.

Description.—*Female (n = 3):* Body robust and elongate, L/W = 3.1. Abdomen with tergites moderately sclerotized and with net- or scale-like ornamentation, pleural membrane between each tergite longitudinally striate. Tergal chaetotaxy: 11: 11: 10: 11: 13: 12: 12: 13: 12: 12: 10: 2, setae subclavate.

Sternites IV–XI moderately sclerotized; all divided except sternite XI; each sternite with small microlyrifissures anteriorly. Anterior genital operculum with 26 small and slender setae; grouped in a triangle; posterior operculum with 9 basal setae. Chaetotaxy of sternites IV–XII 8: 15: 14: 14: 15: 15: 13: 12: 2; setae long and slender.

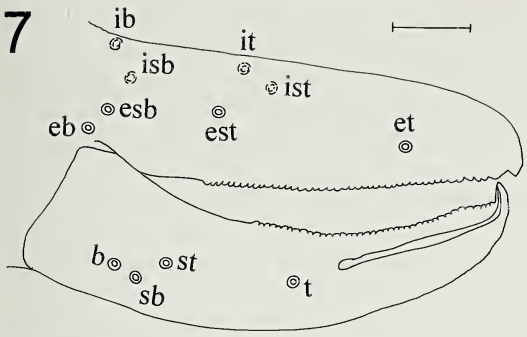
Carapace rectangular, narrowed anteriorly, L/W = 1.02, moderately sclerotized and strongly granulated, with 2 eyespots; distal margin with 6 subclavate setae; proximal margin with 10 setae; and the remainder with 46 similar setae (Fig. 1).

Chelicera slender, L/W = 2.1. Flagellum with 3 blades, largest blade with 4 spines, other blades smooth. Serrula exterior with 24 plates. Galea large, with 6 terminal branches. Hand with 5 setae; *sb* and *b* denticulate (Fig. 3).

Genitalia with H-shaped spermatheca, with 4 lobes: 2 are small and oval, the other 2 spherical and larger (Fig. 5).

Palp robust and reddish brown; trochanter elongate, L/W = 1.15. Femur robust and slender, L/W = 2.3. Patella thin, L/W = 2.1. Chela robust, L/W = 3.15: movable finger elongate and curved, with 54 contiguous marginal teeth and 5 internal accessory teeth, without external accessory in both fingers; trichobothria *b, sb* and *st* at base of finger; *t* near distal end (Fig. 7). Movable finger with terminal venedens (distal venom tooth) and venom duct. Fixed finger with 46 contiguous marginal teeth and 6 internal accessory teeth; all trichobothria situated in basal half of fingers, except for *et* which is situated sub-distally (Fig. 7).

Legs yellowish. Leg I: trochanter wider than long, L/W = 0.9; femur wider than long, L/W = 0.45; patella medium and robust, L/W = 2.7; tibia elongate and thin, L/W = 3.57; tarsus elongate, L/W = 4.5. Leg IV: trochanter L/W = 1.0; femur + patella long and robust, L/W = 2.5; tibia robust, L/W = 4.0;



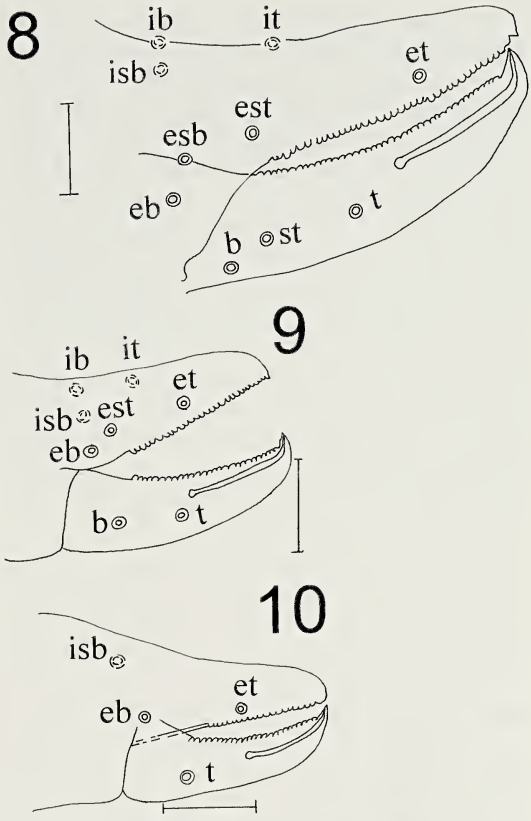
Figures 7–10.—*Pachychernes tamaulipensis* palps. 7. Adult (male); 8. Tritonymph; 9. Deutonymph; 10. Protonymph. Scale lines: 7, 8, 9 and 10 = 0.2 mm. Trichobothrial abbreviations follow Chamberlin (1931) and Harvey (1992).

tarsus robust and short, L/W = 3.8. Tarsi III and IV with a long, prominent tactile seta one fourth length of segment (0.22–0.28) from proximal end, the seta is 0.36 long (Fig. 2).

Measurements of female holotype: Body L 3.403, W 1.071. Carapace L 0.999, W 0.904. Chelicera L 0.384, W 0.184. Palp: trochanter L 0.357, W 0.309; femur L 0.785, W 0.333; patella L 0.809, W 0.38; chela L 1.499, W 0.476; hand L 0.69; movable finger L 0.618. Leg I: trochanter L 0.144, W 0.16; femur L 0.08, W 0.176; patella L 0.476, W 0.176; tibia L 0.4, W 0.112; tarsus L 0.36, W 0.08. Leg IV: trochanter L 0.24, W 0.24; femur + patella L 0.737, W 0.28; tibia L 0.618, W 0.152; tarsus L 0.304, W 0.08.

Measurements of female paratypes (n = 2): Body L 3.4–4.26, W 1.07–1.43. Carapace L 0.97–0.99, W 0.90–0.97. Chelicera L 0.38–0.4, W 0.18–0.20. Palp: trochanter L 0.36–0.38, W 0.28–0.33; femur L 0.78–0.83, W 0.33–0.35; patella L 0.81–0.85, W 0.38–0.40; chela (without pedicel) L 1.43–1.59, W 0.47–0.54, hand L 0.69–0.83; movable finger 0.62–0.71. Leg I: trochanter L 0.14–0.16, B 0.16–0.18; femur L 0.05–0.10, W 0.17–0.21; patella L 0.48–0.50, W 0.17–0.19; tibia L 0.4–0.45, W 0.11–0.12; tarsus L 0.31–0.36, W 0.08. Leg IV: trochanter L 0.24–0.31, W 0.24–0.26; femur + patella L 0.73–0.9, W 0.28–0.35; tibia L 0.59–0.66, W 0.15–0.21; tarsus L 0.30–0.38, W 0.08–0.12.

Male (n = 1): Body elongate. Tergites I–X divided; chaetotaxy 11: 13: 11: 12: 13: 11: 14: 13: 12: 13: 10: 2; setae semiclavate. Sternites moderately sclerotized; IV–X divided; posterior margin of each with many microlyrifissures; chaetotaxy 10: 16: 14: 15: 16: 17: 17: 12: 2. Carapace subtriangular, narrowed anteriorly, strongly sclerotized and granulated. Setae semiclavate, formula 6–12 (58).



Figures 7–10.—Continued.

Genitalia, anterior operculum with 43 setae, without particular order (Fig. 4). Posterior genital operculum with 12 setae; atrium bearing nine short acuminate glandular setae.

Chelicera similar to that of female; with 3 blades in the flagellum; serrula exterior with 24 plates, and 5 setae on the hand, 2 of them (*sb* and *b*) are denticulate.

Palp robust and strongly granulated, reddish-brown in color. Trochanter robust with single protuberance on external face, L/W =1.08. Femur long and robust, L/W = 2.37. Patella robust, L/W = 2.21. Chela very heavily sclerotized, with very long, terminally denticulate setae. Movable finger curved with trichobothria *b, sb* and *st* situated in basal half of finger, trichobothrium *t* slightly distal of middle of finger; with 52 contiguous marginal teeth and 7 internal accessory teeth; only this

finger with venedens and venom duct. Fixed finger with 47 contiguous marginal teeth and nine internal accessory teeth. Without external accessory teeth in both fingers as in female.

Legs robust and yellowish. Leg I: trochanter wider than long, L/W = 0.91; femur short and robust, L/W = 0.26; patella robust and long; L/W = 2.7; tibia and tarsus thin and long, L/W = 3.8 and L/W = 4.3 respectively, both segments with numerous long and acuminate setae (Fig. 6). Leg IV: trochanter rectangular, L/W = 0.93; femur + patella robust, L/W = 2, surface scale-like; tibia robust and long L/W = 3.1; tarsus robust and long, L/W = 3.12. Tarsi III and IV with 1 long, prominent tactile seta near the middle, 0.34–0.35 length of segment from proximal end (TS), seta measured 0.38.

Measurements of male paratype: Body L 3.02, W 0.99. Carapace L 0.88, W 0.72. Chelicera L 0.34, W 0.16. Palp: trochanter L 0.31, W 0.28; femur L 0.76, W 0.32; patella L 0.83, W 0.38; chela (without pedicel) L 1.43, W 0.48, hand L 0.67; movable finger L 0.62. Leg I: trochanter L 0.17, W 0.18; femur L 0.10, W 0.18; patella L 0.48, W 0.18; tibia L 0.38, W 0.12; tarsus L 0.38, W 0.08. Leg IV: trochanter L 0.20, W 0.21; femur + patella L 0.67, W 0.33; tibia L 0.55, W 0.18; tarsus L 0.33, W 0.10.

Tritonymph (n = 7): Similar to adults, particularly females; differing mainly in being smaller and having only 3 trichobothria on the movable finger and 7 on the fixed finger (Fig. 8).

Body long and narrow, L/W = 3.4. Tergites weakly sclerotized, with scale-like ornamentation. Each tergite divided except the last; pleural membranes between them longitudinally striate. Tergal chaetotaxy 10: 9: 9: 10: 12: 9: 9: 12: 11: 9: 10: 2, setae of tergite XI very long. Sternites IV–X divided and lightly sclerotized. Sternites with microlyrifissures between each seta. Sternal chaetotaxy II–XI: 7: 7: 7: 13: 12: 13: 11: 11: 13: 10: 2; XI with ten long setae.

Carapace rectangular, L/W = 1.12, light yellow, strongly granulated, with eye-spots. Setae short and clavate, formula 4–6(40). Chelicera elongate, L/W = 1.85, with 5 setae on hand; flagellum with 3 blades; serrula exterior with 20 plates. Galea robust and long with 5 distal branches. Palp: trochanter short and subquadrate, L/W = 1.04, strongly granulate. Femur long and broad, L/W = 2.1. Patella robust, L/W = 1.92. Chela short and robust, L/W = 2.84, fingers short and slightly curved. All segments with short, clavate setae. Movable finger with 3 trichobothria, lacking trichobothrium *sb*; with 40–44 contiguous marginal teeth and 5 internal accessory teeth; only this finger with venedens and venom duct. Fixed finger has 36 contiguous marginal teeth and 6 internal accessory teeth; with 7 trichobothria, lacking trichobothrium *ist* (Fig. 8). Legs similar to adults, robust and long, surface scale-like, especially on legs III and IV. Tarsi III and IV with 1 long, prominent tactile seta.

Measurements: Body L 2.77 ± 0.15 (2.52–2.97), W 0.81 ± 0.12 (0.59–0.95). Carapace L 0.73 ± 0.05 (0.69–0.83), W 0.65 ± 0.05 (0.59–0.71). Chelicera L 0.27 ± 0.019 (0.25–0.31), W 0.14 ± 0.018 (0.12–0.16). Palp: trochanter L 0.24 ± 0.017 (0.24–0.28), W 0.23 ± 0.027 (0.19–0.28); femur L 0.56 ± 0.043 (0.499–0.595), W 0.26 ± 0.034 (0.24–0.33); patella L 0.56 ± 0.055 (0.50–0.59), W 0.29 ± 0.037 (0.24–0.33); chela L 1.15 0.04 (1.10–1.19), W 0.40 ± 0.032 (0.36–0.45), hand L 0.55 ± 0.049 (0.47–0.59); movable finger L 0.46 ± 0.035 (0.40–0.49). Leg I: trochanter L 0.11 ± 0.009 (0.10–0.13), W 0.13 ± 0.012 (0.12–0.15); femur L 0.08 ± 0.006 (0.06–0.08), W 0.148 ± 0.007 (0.14–0.16); patella L 0.32 ± 0.016 (0.30–0.34), W 0.14 ± 0.035 (0.12–0.22); tibia L 0.26 ± 0.034 (0.22–0.32), W 0.09 ± 0.011 (0.08–0.10); tarsus L 0.25 ± 0.008 (0.24–0.26), W 0. 074 ± 0.003 (0.07–0.08). Leg IV: trochanter L 0.16 ± 0.010 (0.14–0.18), W 0.19 ± 0.022 (0.15–0.22); femur + patella L 0.57 ± 0.037 (0.50–0.59), W 0.26 ± 0.029 (0.22–0.31); tibia L 0.43 ± 0.036 (0.4–0.48), W 0.14 ± 0.023 (0.12–0.18); tarsus L 0.26 ± 0.017 (0.24–0.28), W 0.09 ± 0.012 (0.08–0.11).

Deutonymph (n = 2): Similar to adult but smaller, with 2 trichobothria on movable finger and 6 on fixed finger. Cheliceral hand with 4 setae, lacking seta *sb*.

Body long and narrow, L/W = 3.02. Tergites I–X divided, chaetotaxy: 7: 6: 6: 7: 6: 7: 7: 6: 6: 6: 6: 2, last tergite with long setae. Sternites lightly sclerotized and divided except the last; chaetotaxy: 4: 6: 8: 9: 8: 8: 8: 8: 7: 2. Carapace subrectangular, L/W = 0.98, lightly sclerotized and strongly granulated; with 2 eye-spots near anterior margin and 6

setae; chaetotaxy 6–6 (41). Chelicera long and robust, L/W = 1.75; hand with 4 setae, seta *sb* absent; serrula exterior with 17 blades. Galea elongate, distally bifid. Palp robust, lightly sclerotized and strongly granulated. Chela reddish-brown, L/W = 2.9. Fingers gently curved, movable finger with 2 trichobothria, lacking *sb* and *st* (Fig. 9); with 29 contiguous marginal teeth and 1 internal accessory tooth; only this finger with venedens and venom duct. Fixed finger with 6 trichobothria, lacking *esb* and *ist* (Fig. 9), with 29 contiguous marginal teeth and 3 external accessory teeth. Legs robust and long, similar to those of adults, lightly sclerotized and yellowish. Tarsi III and IV with 1 long, prominent tactile seta.

Measurements: Body L 1.83–2.04, W 0.595–0.69. Carapace L 0.45–0.52, W 0.404–0.476. Chelicera L 0.17–0.22, W 0.10–0.12). Palp: trochanter L 0.16–0.17; W 0.16; femur L 0.29–0.36, W 0.176; patella L 0.32–0.34, W 0.22–0.24; chela L 0.71–0.81, W 0.24–0.28), hand L 0.33–0.36; movable finger L 0.31. Leg I: trochanter L 0.08–0.09, W 0.09–0.10; femur L 0.04–0.05, W 0.09–0.10; patella L 0.17–0.22, W 0.09–0.10; tibia L 0.17–0.18, W 0.06; tarsus L 0.17–0.18, W 0.05. Leg IV: trochanter L 0.08–0.10, W 0.12; femur + patella L 0.352, W 0.168; tibia L 0.24, W 0.088; tarsus L 0.18, W 0.06.

Protonymph (n = 1): Similar to deutonymph in most characters, but smaller, with 1 trichobothrium on movable finger and 3 on fixed finger; cheliceral hand with 4 setae, but galeal seta absent.

Body long and narrow, L/W = 3.4. Carapace rectangular, lightly sclerotized and strongly granulated; anterior margin with 2 eye-spots; anterior and posterior margins with 6 setae each, and 19 on remaining surface. Tergites I–X divided; chaetotaxy, I–X 6, XI 5, XII 2. Sternites, divided except the last; chaetotaxy as for tergites. Chelicera long and broad, L/W = 1.6; hand with 4 setae, lacking seta *sb,* with 3 blades in flagellum, serrula exterior with 13 blades; galea robust and long, with 3 terminal branches. Palp short and robust, yellowish, lightly sclerotized and strongly granulated. Trochanter rectangular, L/W = 1.2, femur short and robust, L/W = 1.5, patella robust, short, widening anteriorly, L/W = 1.36. Chela reddish-brown, movable finger curved with venedens and venom duct, 27 contiguous marginal teeth and with only 1 trichobothrium (*t*) (Fig. 10). Fixed finger with 25 contiguous marginal teeth and 3 trichobothria, *eb, isb* and *et* (Fig. 10). Legs are robust and short, lightly sclerotized and yellowish, similar to later stadia; tarsi III and IV with a long and prominent tactile setae.

Measurements of deuteronymphs: Body L 1.47, W 0.43. Carapace L 0.38, W 0.48. Chelicera L 0.16, W 0.10. Palp: trochanter L 0.14, W 0.11; femur L 0.24, W 0.16; patella L 24, W 18; chela L 0.57, W 0.24, hand L 0.27; movable finger L 0.24. Leg I: trochanter L 0.08, W 0.07; femur L 0.05, W 0.08; patella L 0.14, W 0.08; tibia L 0.12, W 0.05; tarsus L 0.13, W 0.04. Leg IV: trochanter L 0.09, W 0.08; femur + patella L 0.25, W 0.12; tibia L 0.17, W 0.08; tarsus L 0.15, W 0.06.

Remarks.—*Pachychernes tamaulipensis* can be distinguished from *P. baileyi*, *P. attenuatus* and *P. zehorum* due to its smaller size (Feio 1945; Hoff 1946; Muchmore 1990a); it has a single faint transverse furrow on the carapace, instead of two distinct furrows; and it lacks external accessory teeth on the chelal fingers. The pedipalpal femur and carapace length of *P. tamaulipensis* (♀ 0.78–0.83, 0.97–0.99; ♂ 0.76, 0.88) are smaller than in *P. baileyi* (♀ 1.10, not stated; ♂ 1.02, not stated), *P. attenuatus* (♀ 1.33–1.37, not stated; ♂ 1.38–1.51, 1.21–1.26), and *P. zehorum* (♀ 1.04–1.12, 1.21–1.35; ♂ 1.04–1.10, 1.12–1.23); but are slightly bigger than in *P. shelfordi* (♀ 0.72, 0.89; ♂ not stated, not stated). *Pachychernes tamaulipensis* has 24 blades on the serrula externa, *P. baileyi* has 26–28 blades, *P. attenuatus* with 22–24 blades and *P. shelfordi* has 19–21 blades, *P. zehorum* no reported. Like other members of the genus, the spermatheca are H-shaped with 4 lobes, as in *P. baileyi* (Mahnert 1979: fig 118), *P. shelfordi* (Muchmore 1975: fig 9) and *P. attenuatus* (Muchmore 1990a: fig 6). In *P. tamaulipensis* the posterior margin of the carapace is weakly sclerotized, posterior margin very pale, like the genus *Parachernes* (Muchmore & Alteri 1974, see figs. 4, 8) but without a median keel, and with minute triangular scale-like markings.

ECOLOGY

Pseudoscorpions usually live in places with high humidity and moderate temperatures to avoid dehydration (Weygoldt 1969). Rodent nests provide adequate conditions of temper-

ature and humidity (Furman 1968) to sustain populations of pseudoscorpions. Pseudoscorpions associated with nests are found in the nest components more protected from desiccation, like the feeding chamber and nest proper (Montiel-Parra et al. 2001). Nevertheless, *Pachychernes tamaulipensis* was found almost exclusively in the cover, probably because the nests are built in very thick thorny brush where sunlight does not reach the base of the trees; thus, the cover materials remain very moist and provide a suitable habitat.

All specimens of *P. tamaulipensis* were found on the cover of four of the five nests sampled, except for one specimen in the feeding chamber. We found all life stages of *P. tamaulipensis* and for this reason we consider this species to be a permanent inhabitant of these nests. Together with *P. tamaulipensis*, we also found two deutonymphs of the cosmopolitan species *Chelifer cancroides* (Linnaeus 1758) sharing the same habitat. The presence of these nymphs is considered accidental, presumably having arrived at the nests in the material carried by the wood rat to build the cover.

These are the first records of pseudoscorpions in nests of *Neotoma micropus* from México. There are three such records from the United States, the species concerned being *Levichelifer fulvopalpus* (Hoff 1950), *Hesperochernes molestus* (Hoff 1956) and *Dinocheirus texanus* (Hoff & Clawson 1952).

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A NEW SPECIES BELONGING TO THE *VAEJOVIS PUNCTIPALPI* GROUP (SCORPIONES, VAEJOVIDAE) FROM SOUTHERN MEXICO

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ABSTRACT. A new species, *Vaejovis atenango*, belonging to the *V. punctipalpi* group is described from southern Mexico; this group was previously only known from the North American deserts in the USA and northern Mexico. This geographically discontinuous distribution is similar to that observed in the scorpion genus *Hadrurus* Thorell 1876 (Scorpiones, Iuridae).

RESUMEN. Se describe una nueva especie, *Vaejovis atenango*, del grupo *V. punctipalpi* del sur de México; este grupo solo se conocía de los desiertos de Norte América en los EE.UU. y el norte de México. Esta distribución geográfica discontinua es similar a la del género de alacranes *Hadrurus* Thorell 1876 (Scorpiones, Iuridae).

Keywords: Scorpion, taxonomy, Mexico, Guerrero, Morelos

In August 2000 we were invited to attend a field trip to explore Cerro de la Víbora, Municipio de Atenango del Río, Guerrero (~18°14′N, 99°8′W) in southern Mexico. The land rises to 1320m among lowland valleys, was originally covered with low deciduous scrub forest, and it averages slightly less than 1000 m elevation in mostly karstic limestone formations. While black-lighting at night, we made an unexpected discovery: an unusual scorpion, which we immediately recognized as a member of the *Vaejovis punctipalpi* group. This species group contains nine species found in the North American deserts (Sissom 2000): six species in the Sonoran Desert; and two species in the Chihuahuan Desert. Thus, the geographical discontinuity presented by the new species is deemed significant.

The *Vaejovis punctipalpi* group was extensively characterized by Williams (1971). Among its diagnostic features are: (1) carapace with anterior margin essentially straight, and its surface coarsely granular; (2) tergites densely granular, III–VI tricostate (the lateral keels vestigial on some members); (3) sternite VII with one pair of keels (ventral submedian keels obsolete); (4) dorsolateral and lateral supramedian keels on metasomal segments I–IV strongly developed, serrate to crenulate, terminating in an enlarged spine posteriorly; (5) ventrolateral keels strongly developed and crenulate on all metasomal segments; (6) ventral submedian keels usually crenulate on segments II–IV; (7) metasomal segment V longer than movable finger on pedipalps; (8) female genital operculi fused; (9) pedipalp chela swollen, with granular keels; (10) pedipalp fingers short (fixed finger distinctly shorter than carapace), with tips reddish or brown in color; (11) chela trichobothria *ib-it* located near the sixth inner accessory granule; and (12) metasomal segments II–IV distinctly longer than wide (I usually longer than wide, or subequal in males, slightly wider than long in females).

Terminology and methods follow Ponce Saavedra & Sissom (2004). The specimens are deposited in the Colección Nacional de Arácnidos (CNAN), Instituto de Biología, Univer-

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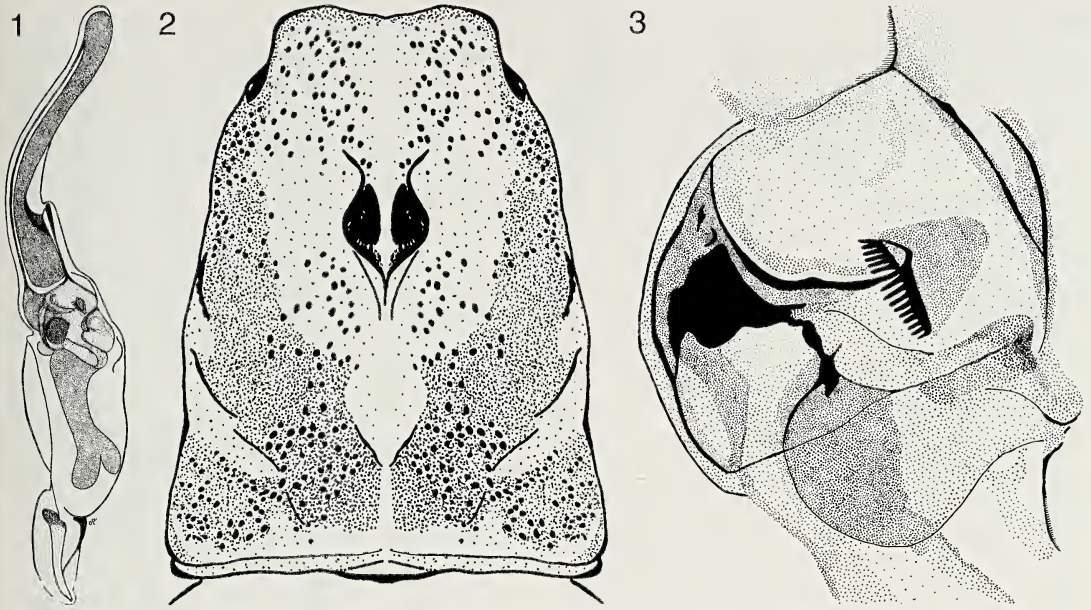


Figures 1–3.—Morphology of the holotype male of *Vaejovis atenango* new species: 1. Lateral view of the left hemispermatophore; 2. Dorsal view of carapace; 3. Lateral view of the ental process of the inner capsular lobe, showing 15 hooklets in the "crown."

sidad Nacional Autónoma de México (IBUNAM).

TAXONOMY

Family Vaejovidae Thorell 1876
Genus *Vaejovis* C.L. Koch 1836

Vaejovis C.L. Koch 1836:51; Sissom 2000:529 (full synonymy).

Type species.—*Vaejovis mexicanus* C.L. Koch 1836 by monotypy.

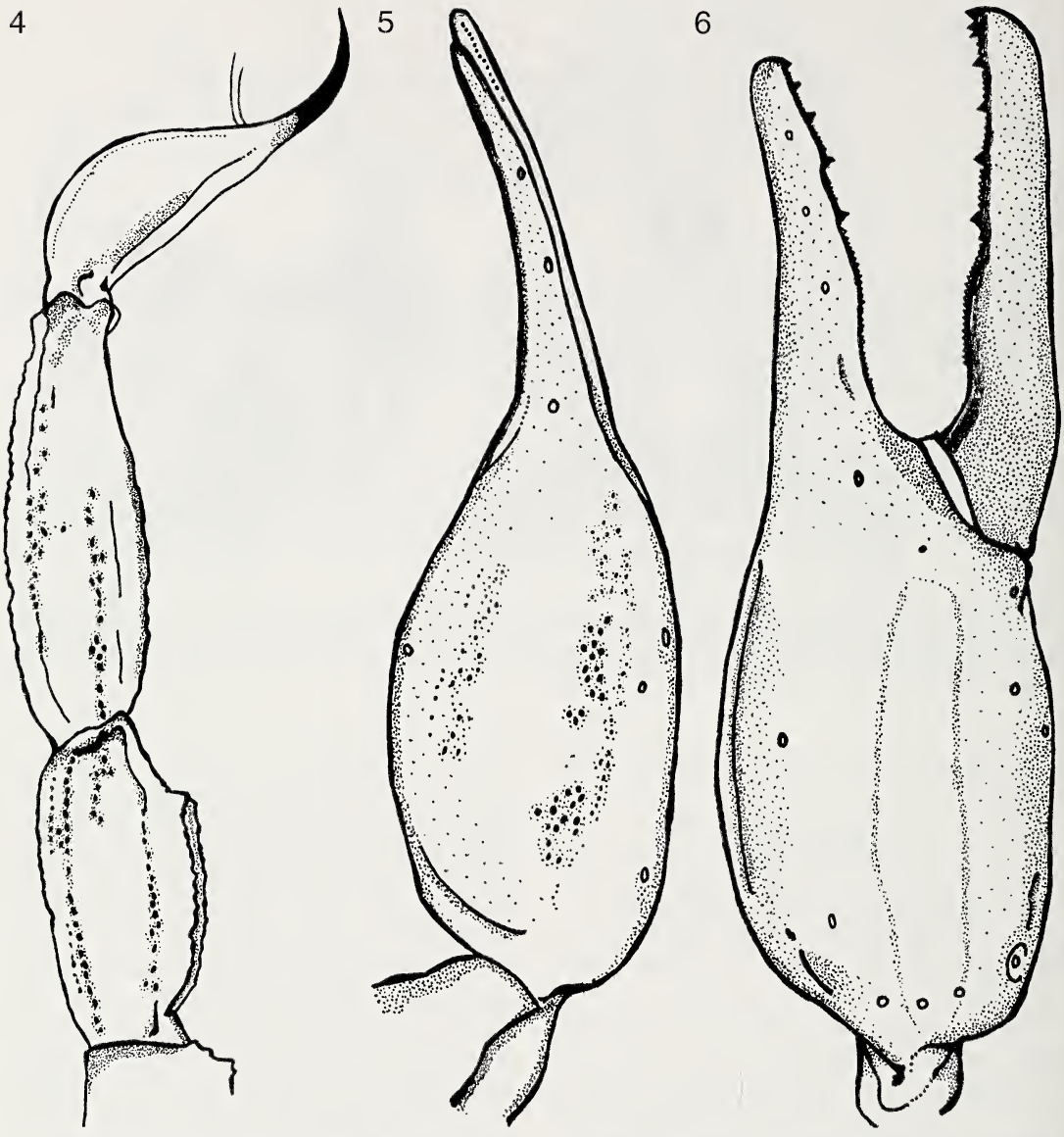
Remarks.—According to Sissom (2000), *Vaejovis* is the largest genus of North American scorpions with approximately 70 species, but it is not monophyletic. It is currently divided into five species groups (see Sissom 2000) which in turn may or may not be monophyletic, plus a number of "unplaced" species. A major systematic revision of the family Vaejovidae is needed, utilizing cladistic arguments, to sort out monophyletic groups and their phylogenetic relationships.

Vaejovis atenango new species
(Figs. 1–6)

Type material.—MEXICO: *Guerrero:* Adult male holotype, 15 km N of Atenango del Río, Municipio Atenango del Río, 18°07.548′N, 99°05.393′W, 651 m, 17 August 2000, M. Capes, O. Delgado, O. Francke, and E. González (CNAN-IBUNAM). Paratypes: MEXICO: *Guerrero:* 1 adult female, 2 adult males, 3 juvenile females, and 10 juvenile male, collected with holotype (CNAN-IBUNAM); 1 adult male, Mirador del Río Balsas, 17°55.082′N, 99°20.085′W, 25 August 2002, Y. Gadar (CNAN-IBUNAM); 1 adult female, La Cubetera, Municipio Valerio Trujano, 21 June 1964, no collector (CNAN-IBUNAM); *Morelos:* 1 adult male, Unidad Progreso, Jiutepec, 18°52.800′N, 99°90.000′W, 1330 m, 2 August 2003, M. Córdova, A. Jaimes and A. Villalba (CNAN-IBUNAM); 1 juv., Colonia Miraflores, Jiutepec, 18°52.800′N, 99°90.000′W, 1330 m, 26 June 2005, M. Córdova (CNAN-IBUNAM).1 adult male, Cerro la Quebradora, Cañón de Lobos, Carretera Jiutepec-Cuautla, Municipio Jiutepec, 18°50.400′N, 99°8.400′W, 11 August 2004, M. Córdova (CNAN-IBUNAM);

Etymology.—The specific name is a noun in apposition taken from the type locality, Atenango del Río, Guerrero, Mexico.

Diagnosis.—The new species is a member of the *V. punctipalpi* group as diagnosed above, which can be separated from the other species of *Vaejovis* in this group by the following combination of characters. Adult males with moderate scalloping in the pedi-



Figures 4–6.—Morphology of the holotype male of *Vaejovis atenango*: 4. Lateral view of metasomal segments IV–V and telson; 5. Dorsal view of right pedipalp chela; 6. External view of right pedipalp chela.

palp chela fingers, leaving a distinct gap when fingers closed; females without scalloping or gap. Pedipalp chela with carinae weak to vestigial, developed as broad, low granular ridges rather than sharp keels. Fixed finger with median denticle row divided into 5 subrows by 4 enlarged denticles. Ventral submedian carinae on metasomal segments I–II weak to vestigial, smooth; on III–IV weak, smooth basally and finely serrate distally. Hemispermatophore inner capsular lobe with "crown" of 15 spines or hooklets, median lobe with sclerotized apophyses.

Description.—*Holotype male: Coloration (in alcohol):* Base color of the pedipalps, chelicerae, legs and metasoma yellowish; mesosoma with faint dusky longitudinal stripes on tergites; fingers of the pedipalp chelae yellowish orange. Aculeus reddish.

Prosoma: Carapace longer than wide (Fig. 1); ratio of carapace length/metasomal segment V length 0.8. Anterior margin weakly

bilobed. Median ocular tubercle slightly raised above carapacial surface. Carapace densely, coarsely granular. Frontal margin of carapace with three pairs of setae.

Mesosoma: Median tergal carina on I and II weak and smooth, on III–VI moderately developed, smooth to crenulate; lateral keels vestigial, represented by a few granules interspersed on a densely granular surface, highlighted by dusky markings. Tergites covered densely with fine granulation on central two-thirds, sides coarsely granulate. Pectinal tooth count 17–18. Sternites III–VII densely punctate. Sternite VII finely granulose, with one pair of moderately strong, crenate lateral carinae.

Hemispermatophore: Distal lamina approximately 15% longer than trunk. Broad flange present forming with distal lamina a distinctive round notch. Ental process of the inner capsular lobe (sperm plug *sensu* Sissom & Stockwell 1991) with "crown" of 15 spines or hooklets. Median lobe with sclerotized apophyses (Figs. 2–3).

Metasoma: Segment I as long as wide; III length/width 1.4; V length/width 2.8. Dorsolateral and lateral supramedian carinae on segments I–IV strong, with large, serrate irregular denticles; distal denticle moderate, not pointed. Lateral inframedian carinae on I complete, strong, crenato-serrate; on II present on distal 1/4 only, strong, serrate; on III weak, present as few granules distally; on IV absent. Ventrolateral carinae on I–IV strong, serrate-crenulate. Ventral submedian carinae on I vestigial, smooth; on II vestigial and smooth basally, weak and faintly serrate on distal third; on III weak, smooth basally, serrate on distal half; on IV moderately strong, crenulate to serrate. Segment V (Fig. 4): dorsolateral carinae strong, granular, serrate on distal third; lateromedian carinae strong, serrate on basal half, then weakening to disappear in distal third; ventrolateral and ventromedian carinae strong, serrate. Metasomal carinae setation: I–IV dorsolateral 1:2:3:3, lateral supramedian 0:2:2:4, lateral inframedian 1:0:0:0, ventrolateral 2:2:2:3–2, ventral submedian 3:3:3:3; segment V, dorsolateral 6, lateral 3/4, ventrolateral 7, ventromedian 5/4. *Telson:* Aculeus represents 1/4 total length; ventral surface with 11 pairs of regular setae, not covered with long fine hairs.

Pedipalps: Femur: length/width ratio 3.1; tetracarinate, dorsointernal, dorsoexternal and ventrointernal carinae strong, granular, ventroexternal carina vestigial, with few moderate granules basally. Internal face with 5–7 subconical granules. Ventral and dorsal surfaces covered densely with fine granules and scattered moderate granules. Orthobothriotaxia C.

Patella: length/width ratio 2.9; tetracarinate, dorsointernal and ventrointernal carinae strong, granular, dorsoexternal and ventroexternal carinae moderate, crenulate. Internal face with 4–5 subconical granules arranged in a longitudinal row. All surfaces densely covered with fine granules. Orthobothriotaxia C.

Chela (Figs. 5–6)*:* Length/width ratio 3.3. Ratio fixed finger length/carapace length 0.6. Dorsal marginal, dorsal secondary, digital and ventrointernal carinae present as rounded ridges covered with fine granulation; dorsointernal carinae as a prominent ridge covered with fine granulation and a few moderate granules; external secondary, ventromedian, ventrointernal carinae present as rounded ridges covered with fine granulation. Dentate margin of fixed finger with primary row divided into five subrows by four enlarged denticles; six inner accessory denticles. Dentate margin of movable finger with primary row divided into seven subrows; apical subrow consisting of a single denticle; seven inner accessory granules, the distal one paired with single apical subrow denticle. Dentate margin of fingers with moderate scalloping; leaving a distinct gap when fingers closed. Orthobothriotaxia C.

Legs: Ventromedian spinule row of telotarsus distally with four prolateral and three retrolateral enlarged spinules flanking the main spinule row.

Measurements of holotype (mm): Total L 53.1; carapace L 6.1; mesosoma L 13.9; metasoma L 25.7: segments: I L/W 3.4/3.4; II L/W 4.1/3.4 III L/W 4.4/3.2; IV L/W 5.8/3.1; V L/W 8/2.9. Telson L 7.4; vesicle L/W/D 4.9/3.2/1.9; aculeus L 2.5; Pedipalps: femur L/W 5.3/1.7; patella L/W 5.8/2.0; chela L/W/D 9.5/2.9/3.1; fixed finger L 3.9; movable finger L 5.4; palm L 4.1.

Measurements of paratype female: Total L 56.6; carapace L 7; mesosoma L 16; metasoma L 34: segments: I L/W 3.4/3.6; II L/W 3.9/3.6; III L/W 4.4/3.4; VI L/W 5.9/3.2; V L/W 8.3/3.2. Telson L 7.6: vesicle L/W/D 5.1/2.9/2.2; aculeus L 2.7; Pedipalps: femur L/W 5.6/2; patella L/W 6.5/2.8; chela L/W/D 10.7/

3.2/3; fixed finger L 4.4; movable finger L 6.1; palm L 4.6.

Intraspecific variability.—In adult females the pedipalp chela fingers lack scalloping and there is no gap when the fingers are closed.

Among 16 males examined, pectinal tooth counts varied as follows: four combs with 16 teeth, 10 combs with 17 teeth, 17 combs with 18 teeth (= mode), and one comb with 19 teeth. Among the six females, we observed two combs with 13 teeth, four combs with 14 teeth and four combs with 15 teeth.

At the type locality, males of this species mature at two different instars, as indicated by their relative sizes: sexually mature males, confirmed by the presence of hemispermatophores, have carapace lengths of 6.1 mm (adult instar = A), 5.1 mm (A-1) and 4.6 mm (A-1), respectively; and there are also sexually immature males at 4.7 mm and 4.5 mm (A-1), respectively, which with a growth factor of 1.3 per molt would attain the size of the sexually mature holotype (Francke & Sissom 1984). Female sample sizes are insufficient for a similar analysis regarding age and size at maturity.

Comparisons.—The *Vaejovis punctipalpi* group as presently recognized has nine species (Sissom 2000). Six species lack scalloping in the pedipalp chela fingers, and the fingers close completely without an apparent gap (*Vaejovis bruneus* Williams 1970, *Vaejovis cazieri* Williams 1968, *Vaejovis crassimanus* Pocock 1898, *Vaejovis hirsuticauda* Banks 1910, *Vaejovis insularis* Williams 1971 and *Vaejovis sonorae* Williams 1971); one species has pronounced scalloping in both males and females, and a large gap is apparent when the fingers are closed [*Vaejovis punctipalpi* (Wood 1863)]; and only two species are similar to *V. atenango* in that males have moderate to weak scalloping and a distinct gap, whereas females lack scalloping and a gap (*Vaejovis magdalensis* Williams 1971 and *Vaejovis russelli* Williams 1971). The fixed finger of *V. magdalensis* has 5 median enlarged granules dividing the median denticle row into six subrows, as opposed to four enlarged granules and five subrows in *V. atenango*. Both *V. magdalensis* and *V. russelli* have moderately to strongly developed granular keels on the pedipalp chela; whereas *V. atenango* has them weakly developed, rounded, and weakly granular.

In Hoffmann's (1931) key to the Mexican species of *Vaejovis*, the new species belongs in the "second section": species with ventral submedian keels present on all metasomal segments, which are smooth on the first three segments. *Vaejovis atenango* differs from *V. intrepidus* Thorell 1876, including its three subspecies, in being smaller in size, lighter in base color, lacking strong granular keels on the pedipalp chelae, and in having only four enlarged denticles on the median row of the fixed finger instead of five. *Vaejovis occidentalis* Hoffmann 1931 also has five enlarged granules on the median denticle row of the fixed finger; metasomal segments I–III wider than long; and seven spines on the hemispermatophore capsular "crown"; whereas *V. atenango* has only four such denticles, metasomal segments II and III distinctly longer than wide, and 15 spines in the hemispermatophore capsular crown. In *V. subcristatus* Pocock 1898, the ventral submedian carinae on metasomal segments I–IV are vestigial and smooth; whereas on *V. atenango* they are weak, smooth on I and II, finely serrate on the distal half of III and IV; in *V. subcristatus* the ventrolateral keels on metasomal segments I–IV are weak and smooth, whereas on *V. atenango* they are moderately strong and finely serrate on all segments; finally, the hemispermatophore capsule in *V. subcristatus* has a crown of only 7–8 spines (Sissom 1989).

Biogeographic considerations.—An interesting parallelism exists between the disjunct distribution of members of the *V. punctipalpi* group, and the distribution of the genus *Hadrurus* Thorell 1876 (family Iuridae Thorell 1876), which has four species mostly in the Baja California Peninsula (one species ranges north across the border into the USA), two species largely in the southwestern USA (one species ranges south across the Mexican border into Sonora), one species in Oaxaca and Puebla, and one species in Guerrero (Sissom & Fet 2000). The last one, *Hadrurus gertschi* Soleglad 1976, was also collected around the foothills of Cerro de la Víbora, Municipio de Atenango del Río, on the same field trip where the new species was found. Therefore, we hypothesize that the same vicariance event, most likely related to the splitting-off of the Baja California Peninsula from the Mexican main-

land, resulted in the discontinuous distributions discussed above.

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THE OLDEST FOSSIL PHOLCID AND SELENOPID SPIDERS (ARANEAE) IN LOWERMOST EOCENE AMBER FROM THE PARIS BASIN, FRANCE

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ABSTRACT. Two new spiders, *Quamtana huberi* new species (Pholcidae) and *Selenops* sp. indet. (Selenopidae), are described from Lowermost Eocene (Ypresian) amber from Le Quesnoy, Oise department, Paris Basin, France. Both specimens represent the oldest known fossils of their respective families. This is the first fossil record of the extant genus *Quamtana*, extending its known geological range by 53 Megaannums (Ma). The known geological age of Pholcidae is extended by approximately 5–10 Ma from that of its previous oldest occurrence in Baltic amber. The known age of Selenopidae and the extant genus *Selenops* are extended by approximately 30 Ma, from their previous oldest occurrence in Dominican Republic amber. The distribution of extant species from these genera suggests the inclusions in amber from the Paris deposit have close affinities with the African fauna.

Keywords: French amber, new species, paleontology, Pholcidae, *Quamtana*, Selenopidae, *Selenops*

France has a diverse fossil spider fauna. Both the oldest known mesothele (Selden 1996) and mygalomorph (Selden & Gall 1992) spiders originate from French sediments. Early reports of French fossil spiders include Gourret (1888) and Berland (1939) who described araneomorph Tertiary fossil spiders from Aix en Provence. Spiders in Cretaceous ambers from France have been known for some time (Schlüter 1978; Néraudeau et al. 2002) but these have yet to be described. Recently, Nel et al. (2004) identified a new source of fossil amber spiders from the Lowermost Eocene of Le Quesnoy in the Paris Basin. The presence of the spider family Oonopidae was reported from this deposit by Penney (2006: text-fig. 2) and the specimen was formally described as *Orchestina parisiensis* by Penney (in press). This paper describes two more specimens from this deposit, which represent the oldest known fossils of the spider families Pholcidae and Selenopidae.

GEOLOGICAL SETTING AND PALEOENVIRONMENT

The amber-bearing strata occur under the River Oise Quaternary deposits at Le Quesnoy, Chevrière (49°21′N, 2°41′E), region of Creil, Oise department, France. They prograde toward the northeast and lie at the bottom of two channels, which cut into the underlying Thanetian marine greensands. The Sparnacian beds consist of a succession of lenticular bodies with two main facies: a) clayed sands rich in frequently pyritized lignite, together with amber, and b) grey clayey sands with less lignite and with a continental vertebrate fauna (Nel et al. 2004). A reconstruction of the paleoenvironment was provided by Nel et al. (1999) and summarized by Nel et al. (2004). Based upon the fossils identified to date, Nel et al. (2004) concluded that 53 Myr ago the region consisted of a fluvial wet forest surrounded by semi-deciduous or deciduous woodland, in a warm climate with wet and dry seasons.

METHODS

The specimens upon which this paper is based are deposited in the Muséum National d'Histoire Naturelle, Paris, France (MNHN). Prior to receipt by the author, the amber piece containing the selenopid had been mounted on a glass microscope slide. All measurements were made using an ocular graticule. Photographs were taken with a Nikon Coolpix 4500 digital camera attached to a Leica M10 stereomicroscope with a 1.6× planapochromatic objective, using a Volpi Intralux 6000 ringlight illuminator inverted on a custom de-

signed base, to produce a 'dark field' effect. CombineZ 5 software was used for computer generation of 3D images, which were then manipulated in Adobe Photoshop. In leg formula (e.g., 1, 2, 4, 3) legs are ranked in order of length, longest first. Abbreviations used in the text and figures: ab = abdomen; ALE = anterior lateral eye; AME = anterior median eye; b = bulb; cda = cheliceral distal apophysis; cla = cheliceral lateral apophysis; cx = coxa; fe = femur; mt = metatarsus; mx = maxilla; p = procursus; pa = patella; PLE = posterior lateral eye; PME = posterior median eye; st = sternum; t = trichobothria; ta = tarsus; ti = tibia; tra = lateral apophysis of palpal trochanter; 1–4 = walking legs 1–4.

SYSTEMATIC PALEONTOLOGY

Family Pholcidae C.L. Koch 1851
Genus *Quamtana* Huber 2003

Type species.—*Quamtana merwei* Huber 2003, by original designation.

Diagnosis.—Long-legged, six- or eight-eyed pholcids with globular, oval or elevated and often posteriorly pointed opisthosoma, varying in total size from 1–4 mm. Distinguished from other genera by the pair of modified hairs on the male cheliceral apophyses (Huber 2003).

Remarks.—This genus is currently known from extant species in sub-Saharan Africa.

Quamtana huberi new species
Figs. 1–3

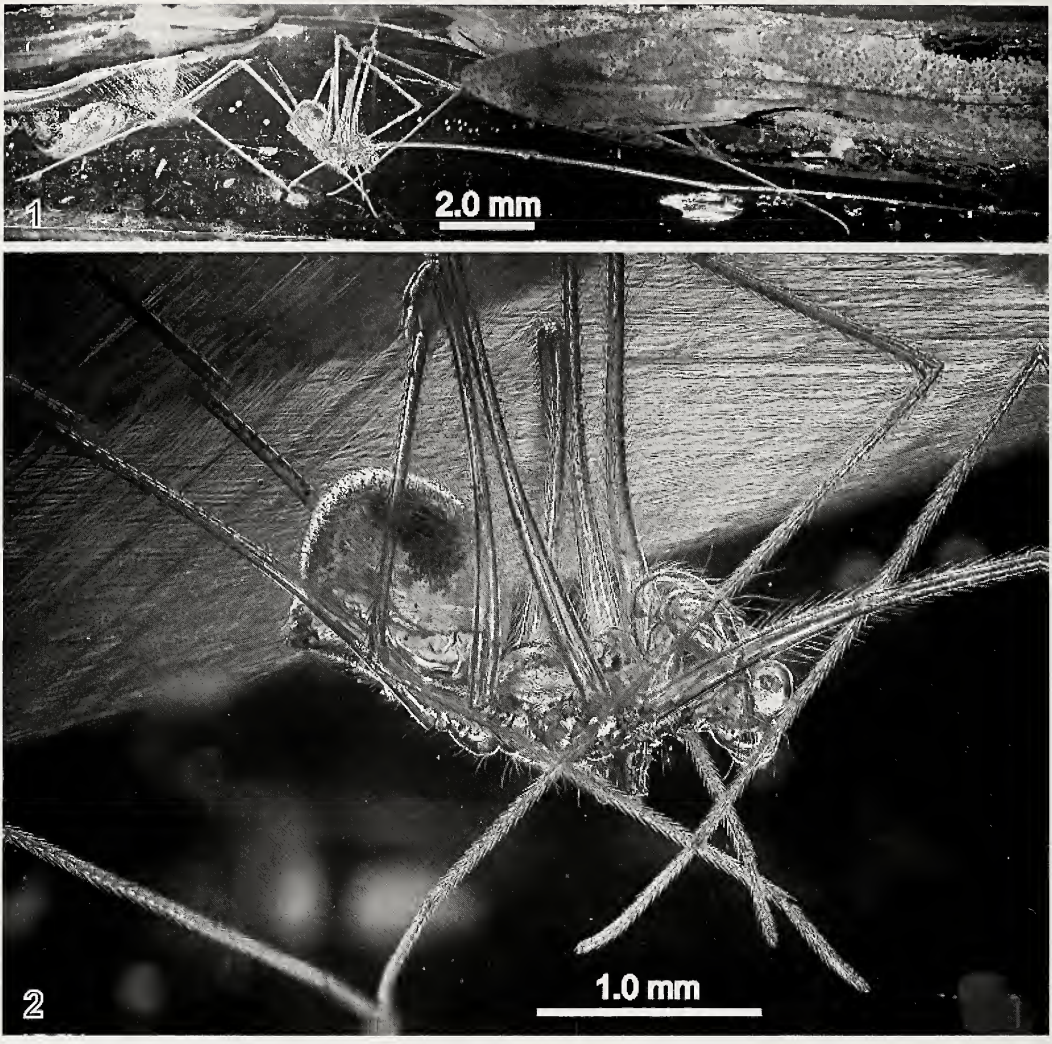
Type material.—Holotype male, Lowermost Eocene amber, Le Quesnoy (49°21′N, 2°41′E), Oise department, Paris Basin, France (MNHN PA 3148).

Etymology.—The specific epithet is a patronym in honor of Dr. Bernhard A. Huber in recognition of his excellent contributions to pholcid spider taxonomy and systematics.

Diagnosis.—The structure of the palpal procursus when examined in retrolateral view distinguishes the new species from all extant species, by the combination of an anteriorly directed finger-like projection located immediately below a posteriorly directed flap-like apophysis.

Description.—Body length 1.58 mm, carapace visible only in lateral view, 0.58 mm long, without any distinguishing features (Figs. 1–3). At least six subequal eyes present in two triads (Figs. 2, 3), the presence or absence of the AME cannot be determined because this region of the carapace, including the clypeus is not clearly visible. Sternum 0.38 mm long. Each chelicera with a proximal lateral apophysis, a proximal anterior apophysis and a distal anterior apophysis with modified hairs (Fig. 3). The presence or absence of a sclerotized cone associated with the distal cheliceral apophysis cannot be determined, but this character is often difficult to observe in Recent specimens and usually requires SEM (Huber 2003). Abdomen globular 1.00 mm long, 0.75 mm high (Figs. 1–3). Legs long (Fig. 1), formula 1,2,4,3; leg 1 fe 4.00 mm, pa 0.25 mm, ti 3.83 mm, mt 5.75 mm, ta 0.98 mm, total 14.81 mm; leg 2 fe 2.50 mm, pa 0.25 mm, ti 2.08 mm, mt 3.00 mm, ta 0.68 mm, total 8.51 mm; leg 3 fe 1.75 mm, pa 0.20 mm, ti 1.35 mm, mt 2.00 mm, ta 0.48 mm, total 5.78 mm; leg 4 fe 2.45 mm, pa 0.23 mm, ti 2.00 mm, mt 2.73 mm, ta 0.48 mm, total 7.89 mm; all lacking spines. Each mt with a trichobothrium located one tenth of the way along from the proximal end of the segment. There also appear to be a maximum of two trichobothria in the proximal region of each ti, although these may be erect setae. Pedipalp, trochanter with a distinct retrolateral apophysis, femur widening distally and patella subtriangular, both without visible modifications. Tibia expanded proximally, narrowing distally, with two trichobothria and two long setae distally. Procursus with an anteriorly directed finger-like projection located immediately below a posteriorly directed flap-like apophysis, distal region not visible; bulb globular, attached prolaterally (Fig. 3).

Remarks.—The new species is tentatively placed in *Quamtana* rather than *Spermophora* Hentz 1841, but this assignment is somewhat problematic due to the invisibility of certain structures in the sole specimen and the absence of females. For example, the chelicerae of male *Quamtana* have a very distinctive pair of modified (pointed, conical) hairs imbedded in the tip of the cheliceral apophyses. The core group of *Quamtana* has an even more distinctive projection of the apophysis accompanying the modified hairs. *Spermophora* has either two or three globular hairs or no modified hairs on the male chelicerae (Huber 2005). The shape of the modified hairs in the fossil specimen cannot be resolved. The proximal



Figures 1–2.—*Quamtana huberi* new species, holotype male, MNHN PA 3148, in Lowermost Eocene amber from Le Quesnoy, Oise department, Paris Basin, France: 1. Lateral view of whole specimen; 2. Lateral view of body region.

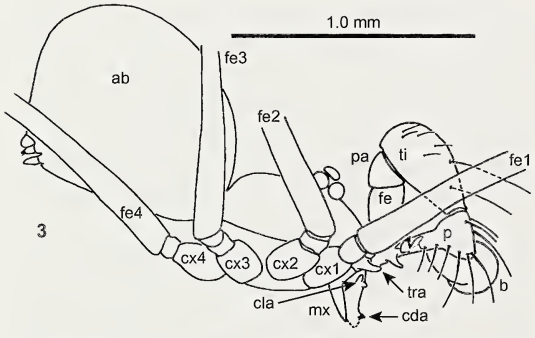


Figure 3.—*Quamtana huberi* new species, holotype male, MNHN PA 3148, in Lowermost Eocene amber from Le Quesnoy, Oise department, Paris Basin, France.

apophyses in the fossil also deserve consideration. It is extremely unusual for pholcids to have two apophyses proximally (Fig. 3), and one case is *Spermophora senoculata* (Dugès 1836). No other *Spermophora* or *Quamtana* species are known to possess two proximal apophyses (B.A. Huber pers. comm. 2005).

In *Quamtana* the palpal bulb sits prolaterally on the tarsus, i.e., looking at the palp ectally the bulb does not project dorsally beyond the tarsus. However, in the fossil the bulb appears to be in a dorsal position. The problem with this character is that the bulb may rotate as an artifact of fixation, such that a prolaterally attached bulb may end up in a dorsal po-

sition (B.A. Huber pers. comm.). *Quamtana* belongs in a group of genera with a very strong sclerite connecting the bulb to the tarsus, but in true *Spermophora* this sclerite is absent. Unfortunately, the relevant region is not visible in the fossil. A ventral flap on the procursus occurs in most *Spermophora* species, but is not known in *Quamtana*. In the core group of *Spermophora*, this flap is sclerotized and serrated (Huber 2005). The fossil possesses a flap similar to *Spermophora* outside the core group. However, *Spermophora* have very distinctive bulbal projections: a serrated apophysis, a hooked apophysis and the embolus. In *Quamtana* there is more variation, but no species is known with a serrated bulbal apophysis (Huber 2003). In the fossil specimen, no bulbal projections can be seen, which argues against placement in *Spermophora*. It can be expected that discovery of new fossil specimens will help resolve the above concerns regarding whether or not the species is correctly placed in *Quamtana*.

Family Selenopidae Simon 1897
Genus *Selenops* Latreille 1819

Type species.—*Selenops radiatus* Latreille 1819 by monotypy.

Diagnosis.—*Selenops* differs from other selenopid genera by the arrangement of the eyes. The AME, PME and ALE aligned or slightly recurved, with the PME equal or subequal in size to AME. Leg 2 > leg 4; ti and mt 1–2 with three, and two pairs of ventral spines respectively (Corronca 2002).

Remarks.—*Selenops* is an extant genus and has been recorded from many parts of the world including the Mediterranean region, Africa, Asia, Australia and the Americas (Platnick 2005).

Selenops sp. indet.
Figs. 4–6

Material examined.—1 juvenile, Lowermost Eocene amber, Le Quesnoy (49°21′N, 2°41′E), Oise department, Paris Basin, France (MNHN PA 2375).

Description.—Body length 1.81 mm, carapace wider than long: 0.74 mm long, 0.81 mm at its widest point, with rounded sides (Figs. 4, 6), with sparse setae and a prominent ocular region. Eight eyes: AME, ALE and PME in a straight line, PLE set further back (Fig. 6). Clypeus and cheliceral structure and dentition not visible. Maxillae longer than wide, labium wider than long, sternum subcircular (Fig. 5), 0.51 mm diameter. Abdomen longer (1.07 mm) than wide (0.59 mm) (Figs. 4, 5), lacking the tufts of white hairs present in some extant species; spinnerets unmodified.

Legs long, laterigrade, formula 2,3,4,1; leg 1 fe 0.57 mm, pa 0.23 mm, ti 0.41 mm, mt 0.24 mm, ta 0.27 mm, total 1.72 mm; leg 2 fe 0.79 mm, pa 0.29 mm, ti 0.57 mm, mt 0.43 mm, ta 0.33 mm, total 2.41 mm; leg 3 fe 0.69 mm, pa 0.29 mm, ti 0.56 mm, mt 0.41 mm, ta 0.31 mm, total 2.26 mm; leg 4 fe 0.71 mm, pa 0.21 mm, ti 0.50 mm, mt 0.40 mm, ta 0.29 mm, total 2.11 mm. The extremely juvenile nature of the specimen makes it impossible to differentiate between true leg spines and other leg setae. Each ti, mt and ta with long trichobothria (Figs. 4–5), tarsi with two claws, prolateral claw distinctly more pectinate than retrolateral claw. Pedipalps unmodified.

Remarks.—Although only a juvenile, this specimen clearly belongs in *Selenops* based on the eye arrangement (Fig. 6), the general habitus and in having legs 2 > legs 4 (Figs. 4, 5).

DISCUSSION

Pholcidae is one of the most diverse spider families with 871 extant species in 75 genera (Platnick 2005), however Huber (2003) estimated that this may represent no more than perhaps 10% of their total global biodiversity. Fossil pholcids are common in Miocene amber from the Dominican Republic, with ten named species described from one fossil genus and three extant genera (Penney & Pérez-Gelabert 2002; Wunderlich 2004). Previous reports of fossil Pholcidae in Baltic amber were discussed by Wunderlich (1986, 2004), but the first unequivocal description of the family from that deposit was by Wunderlich (2004) who described two new species in a new fossil genus. The new species described above represents the oldest fossil record of the extant family Pholcidae, extending its known geological range by approximately 5–10 Ma. This is the first fossil record of the extant genus *Quamtana*, extending its known geological range by 53 Ma. Extant species of *Quamtana* are distributed in sub-Saharan Africa and in South Africa in regions that have > 600 mm annual precipitation (Huber 2003). Though little is known of their behavior and

Figures 4–5.—*Selenops* sp. indet., juvenile, MNHN PA 2375, in Lowermost Eocene amber from Le Quesnoy, Oise department, Paris Basin, France: 4. Dorsal view; 5. Ventral view.

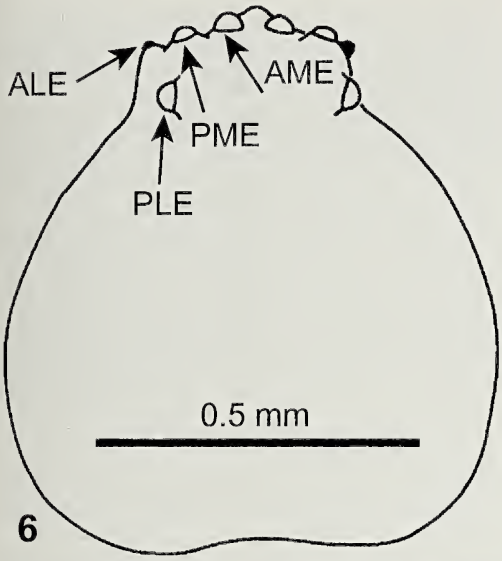


Figure 6.—*Selenops* sp. indet., juvenile, MNHN PA 2375, in Lowermost Eocene amber from Le Quesnoy, Oise department, Paris Basin, France: carapace showing eye arrangement.

ecology, the sparse data available indicate that most extant species live close to the ground, although specimens have been collected by beating vegetation (Huber 2003).

The extant spider family Selenopidae has been described from sub-fossil specimens preserved in Madagascan copal (Bosselaers 2004; Wunderlich 2004; Penney et al. 2005) and from fossil species in Miocene Dominican Republic amber (see Schawaller 1984; Wunderlich 1988, 2004; Penney 2001). However, despite an enormous number (100,000+ Wunderlich, pers. comm. 2004) of Baltic amber fossil spiders studied to date, the family remains unknown from that deposit (e.g., Wunderlich 2004). Thus, the specimen described here more than doubles the known geological age of the family Selenopidae and the extant genus *Selenops*, extending the known geological range of both by approximately 30 Ma.

Both specimens described above belong to extant genera that are highly diverse in Africa today and the extant species of the pholcid genus are restricted to that continent. Thus, the fossil fauna in Lowermost Eocene amber from Paris may have African affinities as occurs with Baltic amber taxa, e.g., the spider family Archaeidae, which has extant species restricted to South Africa and Madagascar. Penney (unpubl. ms.) commented on the absence of Salticidae (jumping spiders) in the Eocene French fauna, in contrast to their frequent occurrence in the Baltic amber fauna. The French amber selenopid described above represents another intriguing difference between these two faunas, which are close both spatially and temporally. However, it would be premature to try and explain these differences until significantly more arthropod taxa have been described from the French deposit, which is currently in the early stages of investigation (Nel 2004).

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LIFE HISTORY AND ECOLOGY OF THE ARMORED SPIDER *MONOBLEMMA MUCHMOREI* (ARANEAE, TETRABLEMMIDAE)

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ABSTRACT. The armored spider *Monoblemma muchmorei* Shear 1978 occurs in the wet subtropical forest of the Caribbean National Forest, Luquillo, Puerto Rico. It is found almost entirely in bamboo litter between 100 and 110 m in elevation and shares this habitat with a number of other species of spiders, ants and other small arthropods. The two sexes come together with no evidence of prior courtship, mate, and may remain *in copula* for many hours. A small decorated egg sac is produced with only one egg in each sac. The female tends the unusually large spiderling for a week or more and appears to offer some protection from other small invertebrates. For reasons not understood, second instar spiders suffered a high mortality rate, up to 70%. In captivity, the adults may live for eight months or more. Observations on the predator-prey interactions among *M. muchmorei* and other small invertebrates are reported. At least 30 species of spiders in 16 families are found associated with *M. muchmorei* in the bamboo litter.

Keywords: Bamboo litter, reproduction, predation, Puerto Rico, leaf litter

Spiders of the family Tetrablemmidae occur in tropical areas around the world and include 30 genera and 130 species (Platnick 2006). The term "armored" refers to the series of separate, latitudinally arrayed sclerites around the abdomen. The genus *Monoblemma* Gertsch 1941 occurs in tropical Africa and the tropical Americas, with several species being found in the Caribbean region (Shear 1978). Nothing has been published on the choice of habitat or the life history on this or any other species of the family.

Monoblemma muchmorei Shear 1978, is a very small (~ 0.9 mm), dark orange-red spider (Fig. 1). This species has been collected in the nearby Virgin Islands, and perhaps in Columbia (Shear 1978). We made our collections in the Caribbean National Forest (CNF), Luquillo, Puerto Rico, in the wet subtropical forest (Ewel & Whitmore 1973). This species was found almost exclusively in bamboo litter (*Bambusa vulgaris* Schrad.) between 100 and 110 m in elevation. We extensively sampled leaf litter, including bamboo litter, from all the principal forest habitats without finding additional specimens. Examples of other habitats sampled include old mahogany plantations at lower elevations, areas dominated by sierra palm at mid elevations, and dwarf forests at higher elevations, each with a different litter type.

METHODS

Beginning in 1992 and continuing to 2004, over 800 forest litter samples were collected in 13 forested study areas, ranging in elevation from 100 to 1065 m in the Caribbean National Forest (CNF) on the mountain El Yunque in Puerto Rico. In so far as possible, each 0.25 m^2 sample was taken within areas of consistent leaf coverage of no less than 1 m^2, including all litter down to the soil surface. Each sample was placed in a cloth bag and subsequently sorted in a large white photo developing tray at the University of Puerto Rico's El Verde Field Station. Often, once the bulk of the larger inert material (leaves, twigs, stones, etc.) had been examined and removed from the tray, the behavior of many organisms, especially of ants and other potential

[1] Deceased

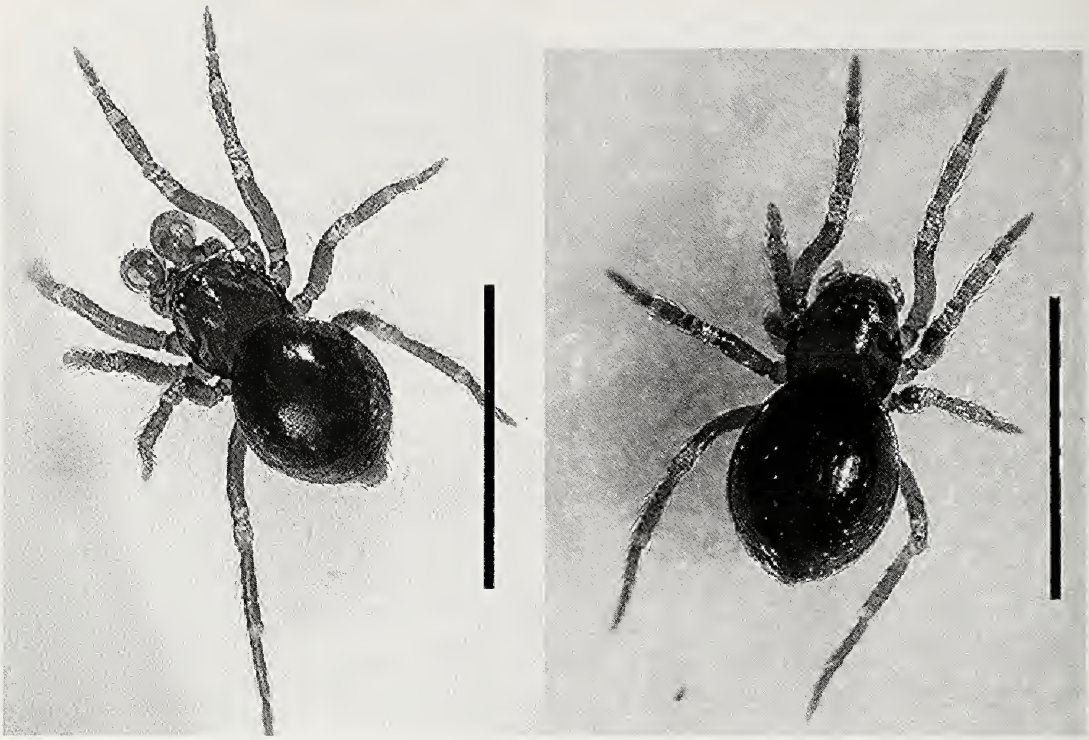

Figure 1.—*Monoblemma muchmorei*. Dorsal views of male (left) and female (right). Scale bars = 1 mm.

predators, was observed. Spiders and other arthropods of interest were preserved in 75% ethanol to be identified and counted later, while specimens of *M. muchmorei* were placed live in Petri dishes for observation.

Live specimens were kept in small plastic culture dishes (47 mm diameter with absorbent pad), some with pieces of moss. Other spiders were kept in larger standard culture dishes (90 mm diameter). Initially the pads of the smaller dishes were moistened with two drops of water. These were in turn kept in larger plastic lidded containers in which damp sponges were also placed to ensure a high humidity. The temperature was maintained between 20–22° C. Pairs also were kept in the smaller dishes to allow closer observation. The larger dishes containing moss were used to keep up to ten or more individuals for various purposes including estimates of longevity and time to maturation. They were fed with the collembolan *Sinella curviseta* Brooks. Individual spiders appeared to require at least one medium sized collembolan every three days. If hungry, spiders immediately seized a collembolan when it was added to the dish whether it fell into webbing or to the bottom of the dish. Specimens were periodically observed for activities that attracted our attention, for example, females engaged in creating webbing, or for interactions between individuals. Images were taken using a Bausch & Lomb trinocular dissecting scope mounted with a Coolpix 960 digital camera.

Angelita Trail area.—The area known as the Angelita Trail was of particular interest as it was here that we found the Tetrablemmidae. The Angelita Trail is at the outer windward edge on the northeastern side of the CNF. It borders the Rio Mameyes and is easily accessed via Route 988. The area ranges from 100–150 m in elevation. The topography is deeply dissected by both intermittent and permanent streams. The forest itself is considered as Tabonuco Forest. It is a mixed, relatively young, second growth forest of uncertain land use history, and includes a variety of trees such as Tabonuco, *Dacryodes excelsa* Vahl., Ausobo, *Manilkara bidentata* (A. D.C.), Motillo, *Sloanea berteriana* Choisy, Guaba, *Inga*

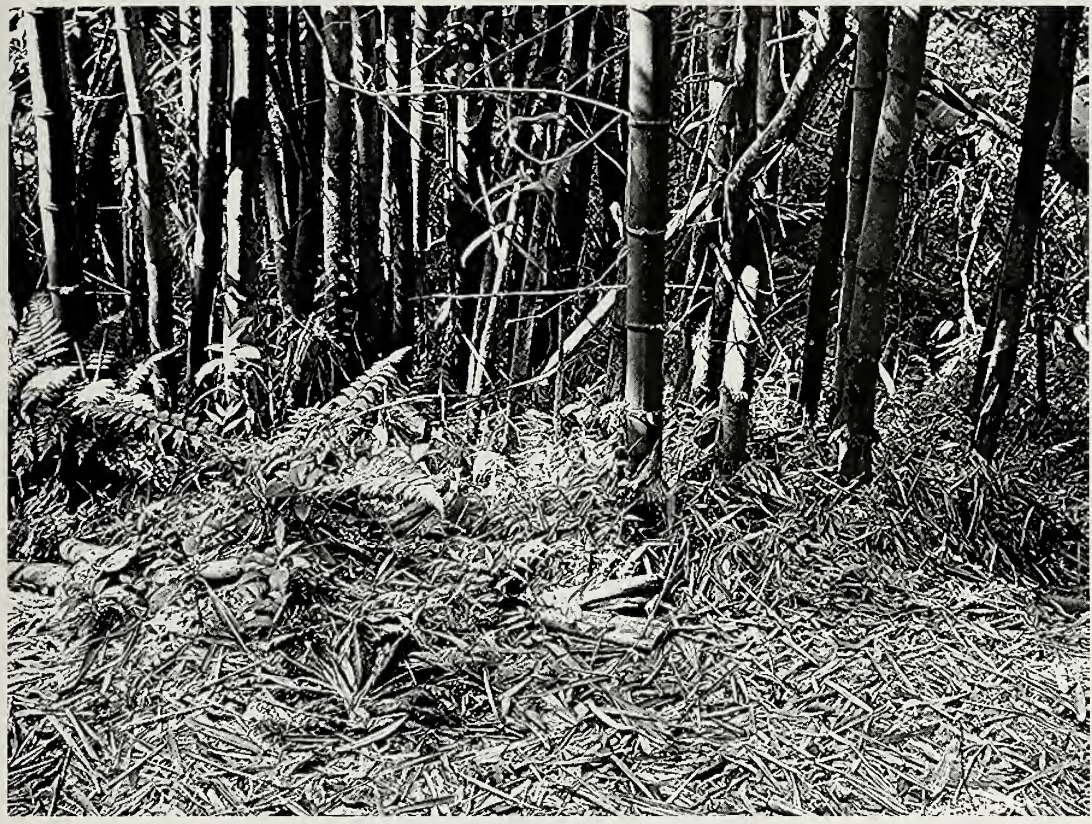

Figure 2.—Stand of *Bambusa vulgaris* at lower end of Anglita Trail, Caribbean National Forest, Puerto Rico.

vera Willd., and Guamà, *I. laurina* (Sw.) Willd. and introduced species such as Bamboo *Bambusa vulgaris* Schrad. and a number of Breadfruit *Artocarpus altilis* (Parkinson). Trumpet-tree *Cecropia peltata* L. is not abundant, suggesting little local hurricane disturbance. There is a highly variable sparse understory. Localized bamboo stands (Fig. 2) occur along the margins of Route 988 and in a loose aggregation of wetter stream-side soils at lower elevations (± 100 m). Unlike most other species of trees in the area, bamboo tends to shed leaves year round. The bamboo litter in areas protected from wind and excessive runoff is usually relatively thick, 1 or more decimeters in depth. Where subject to heavy runoff or flooding after heavy rains, the litter is thin and scattered or absent.

Rainfall averages about 350 cm/yr of which approximately one third is dissipated through evapotranspiration. There are about 100 rain-free days/yr (Garcia-Martino et al. 1996; Weaver 1991). The mean annual air temperature is estimated to be somewhat more than 26° C with the soil temperature about 1° C less. Accordingly, at the lower elevations of the Angelita Trail area, the forest may better be termed a tropical rather than a subtropical forest (Holdridge 1967; Whittaker 1975).

In February 2000, in a transect of deciduous forest litter samples taken along the Angelita Trail, a single specimen of a species of Tetrablemmidae was collected. It was subsequently determined to be *Monoblemma muchmorei*. In February 2001, a similar set of samples was collected, this time with notes taken on each sample's exact locality, including a more detailed description of the leaf litter contained in each sample. No *M. muchmorei* were found. In February 2002 another leaf litter collection was made. When the samples were sorted, once again a single male *M. muchmorei* turned up in a tabonuco leaf sample taken near a clump of bamboo at 110 m. It was noted that no collections had been made exclusively of bamboo litter. So, in December

Figure 3.—Mated pair of *Monoblemma muchmorei*. Male located beneath female. Male's left palp is activated. scale bar = 1 mm.

2002, a special collection of three bamboo litter samples was made near where the specimen had been collected in February. *Monoblemma muchmorei* showed up in abundance. In May 2003 and February 2004, the bamboo litter was extensively sampled with the species occurring in all samples except those where water runoff or flooding had scattered the litter. The bamboo litter at 150 m was extensively sampled in May 2003 and again in February 2004, yielding no specimens of *M. muchmorei*. Over the years a large number of bamboo samples were collected in other study areas from 250–500 m without yielding *M. muchmorei*. Indeed, only a limited number of other species typically found in the forest litter were found in these samples.

Voucher specimens of *M. muchmorei* Shear have been deposited in the Museum of Comparative Zoology, Cambridge, Massachusetts; the U.S. National Museum, Washington, DC; the British Museum of Natural History, London; and the American Museum of Natural History, New York. Voucher specimens of other species collected during this study are maintained in the authors' collection.

RESULTS

Comparison of species present in deciduous forest and bamboo litter.—Thirty spider species from 16 families were taken in the forest and bamboo litter samples between February 2000 and February 2004 (Table 1). The deciduous leaf litter in the Angelita area, from 100 to 150 m in elevation, varied greatly in structure from sample to sample. It was typically less than 1 dm in depth. In contrast to that of bamboo it was usually less densely packed and less permanently positioned, often scattered about by wind and rain. Forest litter

Table 1.—Spider collection data, Angelita Trail area, Caribbean National Forest, Luquillo, Puerto Rico. Each litter sample = 0.25 m^2 from top to soil surface. *n* = number of individuals; m^{-2} = number of individuals per meter square; * = species typically found above litter.

Litter type	Forest						Bamboo					
Date	Feb. 2000		Feb. 2001		Feb. 2002		Dec. 2002		May 2003		Feb. 2004	
Elevation in meters	110–150		100–150		110–150		110		100–110		100–110	
Number of samples	10		10		10		3		9		7	
Total sample area m^2	2.50		2.50		2.50		0.75		0.75		0.75	
Species	*n*	m^{-2}	*n*	m^{-2}	*n*	m^{-2}	*n*	m^{-2}	*n*	m^{-2}	*n*	m^{-2}
Caponiidae												
Nops blandus (Bryant 1942)	—	—	—	—	1	0.4	1	1.3	—	—	—	—
Corinnidae												
Corinna javuyae Petrunkevitch 1930	—	—	—	—	—	—	—	—	—	—	1	0.6
Phrurolithus insularis Petrunkevitch 1930	—	—	—	—	2	0.8	5	6.7	25	11.1	2	1.1
Dipluridae												
Masteria petrunkevitchi (Chickering 1964)	44	17.6	2	0.8	15	6.0	44	58.7	81	36.0	20	11.4
Linyphiidae												
Lepthyphantes microserratus Petrunkevitch 1930	3	1.2	6	2.4	3	1.2	—	—	1	0.4	—	—
Mysmenidae												
Calodipoena caribbaea (Gertsch 1960)	—	—	5	2.0	4	1.6	—	—	1	0.4	1	0.6
Ochyroceratidae												
Ochyrocera sp. 1	—	—	44	17.6	5	2.0	—	—	1	0.4	1	0.6
Theotima minutissimus (Petrunkevitch 1929)	127	50.8	152	60.8	161	64.4	71	94.7	163	72.4	48	27.4
Oonopidae												
Ischnothyreus peltifer (Simon 1891)	—	—	—	—	—	—	—	—	3	1.3	—	—
Oonops castellus Chickering 1971	7	2.8	—	—	7	2.8	7	9.3	7	3.1	5	2.9
Oonops ebenecus Chickering 1972	—	—	—	—	—	—	—	—	7	3.1	6	3.4
Gamasomorpha lutzi Petrunkevitch 1929	—	—	3	1.2	—	—	—	—	—	—	1	0.6
Triaeris stenaspis Simon 1891	—	—	1	0.4	4	0.1	—	—	2	0.9	—	—
Pholcidae												
Modisimus cavaticus Petrunkevitch 1929	37	14.8	6	2.4	—	—	—	—	—	—	2	1.1
Modisimus coeruleolineatus Petrunkevitch 1929	—	—	—	—	7	2.8	—	—	11	4.9	—	—
Modisimus montanus Petrunkevitch 1929	29	11.6	—	—	17	6.8	1	1.3	7	3.1	8	4.6
Prodidomidae												
Neozimiris nuda Platnick & Shadab 1976	1	0.4	—	—	1	0.4	2	2.7	6	2.7	—	—

Table 1.—Continued.

Species	*n*	m^{-2}	*n*	m^{-2}	*n*	m^{-2}	*n*	m^{-2}	*n*	m^{-2}	*n*	m^{-2}
Salticidae												
Corythalia gloriae (Petrunkevitch 1929)*	—	—	—	—	—	—	—	—	—	—	2	1.1
Corythalia signatus (Banks 1890)	1	0.4	—	—	—	—	—	—	—	—	—	—
Emathis portoricensis Petrunkevitch 1930	—	—	—	—	—	—	—	—	5	2.2	—	—
Jollas minutus Petrunkevitch 1930	4	1.6	1	0.4	3	1.2	10	13.3	21	9.3	4	2.3
Sparassidae												
Pseudosparianthis jayuyae Petrunkevitch 1930	—	—	2	0.8	1	0.4	3	4.0	4	1.8	—	—
Stasina portoricensis Petrunkevitch 1930	3	1.2	—	—	—	—	—	—	—	—	1	0.6
Tetrablemmidae												
Monoblemma muchmorei Shear 1976	1	0.4	—	—	1	0.4	67	89.3	170	75.6	42	24.0
Tetragnathidae												
Leucauge regnyi (Simon 1897)*	1	0.4	1	0.4	2	0.8	—	—	—	—	—	—
Theridiidae												
Styposis sp?	—	—	—	—	—	—	2	2.7	6	2.7	1	0.6
Thymoites guanicae (Petrunkevitch 1930)	4	1.6	—	—	1	0.4	5	6.7	—	—	1	0.6
Theridiosomatidae												
Ogulnius gloriae (Petrunkevitch 1930)	—	—	—	—	—	—	—	—	—	—	1	0.6
Theridiosoma nechodomae Petrunkevitch 1930	6	2.4	—	—	4	1.6	—	—	—	—	—	—
Theridiosomatidae sp?	2	0.8	—	—	—	—	—	—	—	—	—	—
Total species	15		11		18		12		18		18	
Total individuals	270		223		239		218		521		147	
Total individuals m^{-2}		108.0		89.2		95.6		87.2		248.1		84.0

seldom developed a near-soil layer of decomposed material. The most abundant species overall were *Theotima minutissimus*, *Monoblemma muchmorei*, and *Masteria petrunkevitchi* respectively.

The relative abundance of each species in each litter type is shown in Table 2, arrayed from those demonstrating the greatest degree of preference for forest litter down to those that prefer bamboo litter. Of those species most commonly found in forest litter, *Ochyrocera* sp? (Ochyroceratidae) is found in larger leaf litter that is much less compact at the surface and the pholcid, *Modisimus cavaticus* (Pholcidae) is found most often in litter that provides pockets of larger open spaces, as under a palm stem, where it produces a substantial web. Such spaces do not normally occur in bamboo litter. By comparison *Modisimus montanus* clearly prefers small spaces like the tightly curled leaves of tabonuco in which to make its web; thus, this species can be found in the more tightly spaced bamboo litter more frequently though it still prefers forest litter. The very small parthenogenetic spider, *Theotima minutissimus* (Ochyroceratidae) was equally present in both types of litter (Edwards et al. 2003). This was consistent with our observations throughout the forest. It tended to be found in wetter litter with more

Table 2.—Comparison of relative abundance of spiders in the two types of litter examined, arrayed in decreasing (relative) order from forest to bamboo litter (far right column). Family names are given in parentheses. The notation "n_f" and "n_b" refer to numbers of spiders in Forest and Bamboo respectively, m^{-2} = number per square meter of litter.

Litter type	Forest	Bamboo		Forest	Bamboo	
Total sample area in m^2				7.50	4.75	
Species name	n_f	n_b	$n_f + n_b$	m_f^{-2}	m_b^{-2}	m_f^{-2}/m_b^{-2}
Ochyrocera sp. 1 (Ochyroceratidae)	49	2	51	6.53	0.42	15.52
Modisimus cavaticus (Pholcidae)	43	2	45	5.73	0.42	13.62
Lepthyphantes microserratus (Linyphiidae)	12	1	13	1.60	0.21	7.60
Calodipoena caribbaea (Mysmenidae)	9	2	11	1.20	0.42	2.85
Stasina portoricensis (Sparassidae)	3	1	4	0.40	0.21	1.90
Gamasomorpha lutzi (Oonopidae)	3	1	4	0.40	0.21	1.90
Modisimus montanus (Pholcidae)	46	16	62	6.13	3.37	1.82
Triaeris stenaspis (Oonopidae)	5	2	7	0.67	0.42	1.58
Theotima minutissimus (Ochyroceratidae)	440	282	722	58.67	59.37	0.99
Nops blandus (Caponiidae)	1	1	2	0.13	0.21	0.63
Thymoites guanicae (Theridiidae)	5	6	11	0.67	1.26	0.53
Oonops castellus (Oonopidae)	14	19	33	1.87	4.00	0.47
Modisimus coeruleolineatus (Pholcidae)	7	11	18	0.93	2.32	0.40
Masteria petrunkevitchi (Dipluridae)	61	145	206	8.13	30.53	0.27
Pseudosparianthis jayuyae (Sparassidae)	3	7	10	0.40	1.47	0.27
Neozimiris nuda (Prodidomidae)	2	8	10	0.27	1.68	0.16
Jollas minutus (Salticidae)	8	35	43	1.07	7.37	0.15
Phrurolithus insularis (Corinnidae)	2	32	34	0.27	6.74	0.04
Monoblemma muchmorei (Tetrablemmidae)	2	279	281	0.27	58.74	0.01
Leucauge regnyi (Tetragnathidae)	4	—	4	0.53	—	—
Corinna jayuyae (Corinnidae)	—	1	1	—	0.21	—
Ischnothyreus peltifer (Oonopidae)	—	3	3	—	0.63	—
Oonops ebenecus (Oonopidae)	—	13	13	—	2.74	—
Corythalia gloriae (Salticidae)	—	2	2	—	0.42	—
Corythalia signatus (Salticidae)	1	—	1	0.13	—	—
Emathis portoricensis (Salticidae)	—	5	5	—	1.05	—
Styposis sp? (Theridiidae)	—	9	9	—	1.89	—
Ogulnius gloriae (Theridosomatidae)	—	1	1	—	0.21	—
Theridiosoma nechodomae (Theridosomatidae)	10	—	10	1.33	—	—
Theridiosomatidae sp?	2	—	2	0.27	—	—
Number of species	23	26	30			
Total individuals	732	886	1618			
Total number m^{-2}				97.60	186.53	

decayed material close to the soil. *Phrurolithus insularis* (Corinnidae) and *Oonops castellus* (Oonopidae) have a slight preference for bamboo litter. The small diplurid (adults ± 5 mm) *Masteria petrunkevitchi* (Dipluridae) also appears to favor bamboo litter. Although it is found in many types of litter on the mountain, *Masteria* usually occurs near the bottom of deeper litter. In many hours of searching we have failed to find any substantial webbing that could be assigned to this species. *Jollas minutus* (Salticidae) clearly prefers denser litter.

Habitat of *M. muchmorei*.—With the two single specimen exceptions noted above, *M. muchmorei* was taken only in bamboo litter near the bottom of the Angelita transect. As noted earlier, unlike most other species of trees in the area, bamboo tends to shed leaves year round. The litter can accumulate to a considerable depth especially on more level ground. *M. muchmorei* occurred most fre-

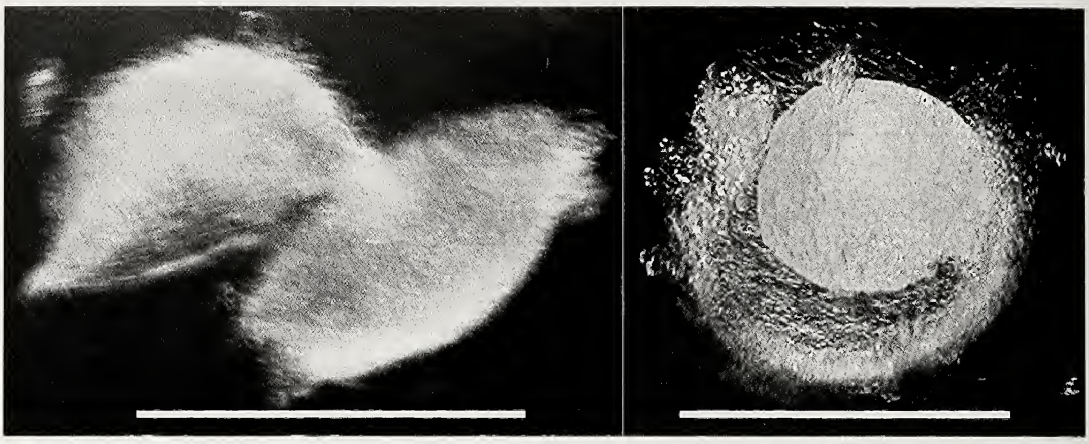

Figure 4.—Egg sac and egg of *Monoblemma muchmorei*. Right: hemispherical top portion and lenticular bottom portion separated. Left: single egg on bottom portion. Note that top and bottom portions separated cleanly. Scale bar = 0.4 mm.

quently in the bamboo litter subject to less disturbance by wind or water. Here the upper layers formed a flatter surface of drier undecayed leaves that acted to shed water. Under this layer there is a transitional layer of leaves that progressively decays down to the soil where the leaves are thoroughly decayed. This is different from the litter composition under the deciduous trees in the forest, where the leaves show less decay at the soil surface. To test if this difference impacted the local fauna, we collected five bamboo litter samples each from the upper relatively undecayed layer and from the transitional decomposing layer beneath. In these samples the upper layer had an average 5.2 (1–11) individuals of *M. muchmorei* and the lower transitional layer had an average of 38 (15–61) individuals. The structure as well as the type of leaf litter dictated the choice of living spaces for *M. muchmorei*. On steep slopes and where wind and water had broken up the litter piles, few if any *M. muchmorei* were found. Of the 141 specimens of *M. muchmorei* counted, females outnumbered the males: females 83 (59%), males 58 (41%).

Behavior and reproduction in *M. muchmorei*.—In December 2002, while at the field station, 3 pairs of adult *M. muchmorei* were placed in small dishes with strands of moss shortly after being captured. Within 1 hour, one pair mated and remained *in copula* for approximately 14 hours (09:30–23:15 h). They came together while walking around on the bottom of the dish. No obvious courtship was observed. The male simply turned venter side up as the female approached from above and wrapped his first legs around the cephalothorax of the female and immediately inserted his right embolus. They remained together with virtually no further movement from that point on. There was no evidence that the palps were alternated.

Subsequently, seven additional matings have been observed. In each case the positions taken between the sexes did not differ significantly from the first observation. Whether on the bottom or side of the dish or once in webbing in moss, the female always approached while the male was venter up. No activity that could be described as courtship was ever observed. Two pairs engaged almost as soon they were placed together. These two engagements lasted 5 and 7 hours. Each male quickly seized the female, wrapping first legs around the cephalothorax, sometimes the second pair of legs as well, on the anterior part of the abdomen. The third pair of legs loosely held the female's abdomen from below (Fig. 3). In all cases the bodies were held so closely together that it was not possible to clearly see how the palps were handled beyond the fact that one palp could usually be seen a little to the side. This suggests that only one palp was ever used. For long periods, often for hours, there was virtually no movement or alternation of the palps.

Where mating had been observed, egg sacs were produced 3–4 weeks later. The white egg sac, ~ 0.4 mm in diameter, has a shallow dish

Figure 5.—Mother, newly emerged spiderling, and decorated egg sac of *Monoblemma muchmorei*.

bottom and tall hemispherical top, with a loosely joined vague equator between the halves (Fig. 4). It was usually decorated with small bits of leaves or moss, typically placed on a surface such as a piece of leaf or vertically on the side of the dish. Hatching occurred approximately 3–4 weeks following the production of the egg sac. In all cases in which there were very small pieces of leaves or other dark material available in the dishes, the females decorated the eggs. In dishes with moss, the females were often found in vaguely woven spherical webs. Only a small amount of silk was used and there was no regular pattern to the webbing. This webbing did not play a significant role in prey capture although collembola were occasionally entangled within. Males were more often wandering about and not remaining in webbing.

Spiderlings emerged by splitting the two halves of the egg sac. Newly hatched (2nd instar) spiderlings were translucent light yellow,

Table 3.—Small invertebrate predator and prey organisms other than spiders (Table 1) usually present in bamboo litter. Most of the species listed were present in all samples in modest numbers, from a few to several dozen. The ants that nested in the litter varied greatly, from small numbers to hundreds.

ARACHNIDA
PSEUDOSCORPIONIDA
Chthoniidae
Tyrannochthonius imitatus Hoff 1959.
Syarinidae
Ideobisium puertoricense Muchmore 1982.
SCHIZOMIDA
Schizomidae
Luisarmasius yunquensis (Camilo & Cokendolpher 1988). Rare.
COLLEMBOLA
Sminthuridae
Ptenothrix borincana Soto-Adames 1988.
Calvatomina nymphascopula Soto-Adames 1988.
Calvatomina rufescens (Reuter 1890).
Entomobryidae
Lepidocyrtus caprilesi Wray 1953.
Pseudosinella violeta Mari Mutt 1986.
Paronellidae
Campylothorax sabana Mari Mutt 1987.
Onychiuridae
Onychiurus (Protaphorura) herus Christiansen & Bellinger 1980.
INSECTA
Formicidae
Ponerinae
Anochetus kempfi Brown 1978.
Odontomachus ruginodis Smith 1937.
Hypoponera opacior Forel 1893.
Formicinae
Brachymyrmex heeri Forel 1874.
Myrmicinae
Pyramica rogeri Emery 1890.
Solenopsis azteca Forel 1893.
Pheidole moerens Wheeler 1908.
Pheidole sculptior Forel 1893.
Monomorium ebeninum Forel 1891.
Wasmannia auropunctata Roger 1863.
Cyphomyrmex minutus Mayr 1862.

~ 0.4 mm length. The first instar skin remained in the bottom part of the egg sac. On emerging, spiderlings immediately went to webbing produced by the female. The female stayed in close proximity for at least a week (Fig. 5). During this time, the females killed any collembola or other small organisms that came near. In one case a pile of 8 large uneaten collembola collected beneath the web.

Second instar spiderlings fed on the smallest collembola, but often appeared to have difficulty subduing its prey. Relatively few progressed to the third instar. The color of the spiderlings progressed to a darker yellow as they matured and only became reddish orange on maturation. The apparent high mortality of the second instar spiders was disturbing although it has been noted that there were also few younger instars found in the litter collections. In other rearing experiments, second instar spiderlings of *Theotima minutissimus*, and *Ochyrocera* sp?. similarly had difficulty feeding and advancing to the third instar. Beyond this stage *Sinella* posed no problem as food for any of these species.

Predation.—In some bamboo samples, the nests of the ant *Wasmannia auropunctata* Roget were often abundant within wetter, inner closely packed litter, sometimes with 25 or more individuals in each nest. *Wasmannia* consistently seized the darkly colored sminthurid collembolan *Ptenothrix borincana* Soto, but not the reddish *Calvatomina rufescens* Reuter. This ant also occasionally seized the larger *Campylothorax sabana* Wrey and in one instance another ant species, *Solenopsis azteca* Forel, as well as the very small spiders *Theotima minutissimus* and *Calodipoena caribbaea* (Mysmenidae). Less abundant but consistently present, another ant, *Monomorium ebeninum* Forel, preyed mainly on *Campylothorax sabana* and other similarly sized and colored collembolans. *Monomorium* also seized very small beetles and once a second instar salticid *Jollas minutus*. In some samples, the ant *Pheidole moerens* Mayr was abundant but was never observed attacking any other living organism. In a large petri dish with an adult female *Styposis* sp? (Theridiidae), eight *M. muchmorei* were captured in *Styposis* webbing. No species of ant paid any attention to *M. muchmorei*. Small numbers of two species of pseudoscorpions, *Tyrannnochthonius imitatus* Hoff and *Ideobisium puertoricense* Muchmore were present in most bamboo and forest litter samples, neither of which were observed to prey on any organism. None of the spiders collected paid any attention to *M. muchmorei*. The various identifiable arthropods observed are listed in Table 3.

Once spiderlings in captivity had achieved the third or fourth instar, they usually survived to maturity. As noted earlier, few second instar spiderlings raised in captivity survived; on average one out of five. Adults brought in from the field survived on average four months. Some died immediately and others lived for as long as six months. Adults that had matured in captivity, however, typically survived from 5–6 mo. One female died at the age of nine months after producing eight egg sacs. We observed no predation on this spider in the field. In captivity, however, they were observed getting entangled in the webbing of other spiders, especially the webs of *Styposis*. Assuming that our inability to successfully get these spiders through to the third instar is not the case in the field, and that they produce only one egg at a time there as well, *M. muchmorei* apparently has a very low natural mortality rate.

DISCUSSION

The very specific choice of habitat by *M. muchmorei* in Puerto Rico as well as the paucity of information in the literature on the habitat of the many species of the family Tetrablemmidae is intriguing. *Bambusa vulgaris* was imported from southeast Asia into the Americas and subsequently into Puerto Rico early in the 19th century (McClure 1993; Londono 2001). It is often used today to stabilize steep areas along roadsides and near streams to reduce erosion in areas that flood. It is worth considering the possibility that *M. muchmorei* was introduced along with the bamboo. We suggest that it would be worthwhile to pay particular attention to bamboo litter worldwide. Further, Lehtinen (1981) has suggested that the genus *Monoblemma* may need to be reexamined. *Monoblemma muchmorei* may belong to another genus and other specimens, including those that Shear examined from Angelica Rock, may be another species, or even a different genus.

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We greatly appreciate the assistance of Ingi Agnarsson, James Cokendolpher, Stefan Cover, William Shear, Mark Harvey, Herbert Levi and Felipe Soto-Adames for determining, confirming and/or updating the systematic status of many of the large array of organisms with which we dealt. Eric Edwards assisted on some field trips and in making observations on captive specimens. Personnel at the El Verde Field Station graciously assisted, including Jill Thompson, Maria Aponte and John Bithorn.

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PSEUDALBIORIX, A NEW GENUS OF IDEORONCIDAE (PSEUDOSCORPIONES, NEOBISIOIDEA) FROM CENTRAL AMERICA

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ABSTRACT. A new genus of Ideoroncidae, *Pseudalbiorix*, is described from Central America, and is found to consist of four species: the type species *P. reddelli* (Muchmore 1982), new combination from southern Mexico, *P. veracruzensis* (Hoff 1945), new combination from Belize, Guatemala and southern Mexico, and *P. muchmorei* Barba & Pérez, new species and *P. armasi* Barba & Pérez, new species from western Cuba. *Pseudalbiorix reddelli* and *P. veracruzensis* are transferred from the genus *Albiorix*. Members of this genus differ from all other ideoroncids principally in the morphology of the chelal externo-distal condyle. All post-embryonic stages of *P. reddelli* are described.

Keywords: Pseudoscorpions, Mexico, Cuba, taxonomy, morphology, new species, biospeleology, troglobite

The pseudoscorpion family Ideoroncidae consists of several genera found in disparate parts of the world (e.g., Harvey 1991; Mahnert 1984). The African fauna comprises three genera, *Negroroncus* Beier 1931, *Nannoroncus* Beier 1955 and *Afroroncus* Mahnert 1981, mostly restricted to the eastern half of the continent (Mahnert 1981), while the Asian fauna consists of the genera *Dhanus* Chamberlin 1930, *Shravana* Chamberlin 1930 and *Nhatrangia* Redikorzev 1938. The family is represented in the Americas by another three genera, *Ideoroncus* Balzan 1887, *Albiorix* Chamberlin 1930 and *Typhloroncus* Muchmore 1979 where a total of 30 species have thus far been named. The majority of American ideoroncid species are found in epigean habitats but some, such as *Ideoroncus cavicola* Mahnert 2001 from Brazil, the four Mexican species of *Typhloroncus*, and several species of *Albiorix*, are restricted to caves.

During research into the ideoroncid fauna of Central America, we have independently recognized the presence of some species that could not be placed within a pre-existing genus. One of these, *Albiorix reddelli* Muchmore 1982, was reluctantly included in *Albiorix* by Muchmore (1982) and Mahnert (1984), but a satisfactory placement could not be found at the time. Our discovery of a further three species, including *A. veracruzensis* Hoff 1945, from various localities across Central America that share important morphological features with *A. reddelli* has enabled us to conclude that this group of species should be recognized as a distinct genus, to which we apply the name *Pseudalbiorix*. The aims of the present paper are to describe the new ge-

nus, to provide descriptions of all four species based upon the abundant new material available to us, and to name two new species of *Pseudalbiorix* from Cuba, including the sole troglobitic species of the genus.

The specimens examined during this study are deposited in the American Museum of Natural History, New York (AMNH), the arachnological collection of Instituto de Ecología y Sistemática (CZACC) of the Ministry of Science, Technology and Environmental of Cuba, the Biospeleological collection of the Cuban Speleological Society, La Habana (ColBK), the California Academy of Sciences, San Francisco (CAS), the Florida State Collection of Arthropods, Gainesville, Florida (FSCA), and the Western Australian Museum, Perth (WAM). All specimens were measured with a micrometer eyepiece on a compound microscope, as described by Chamberlin (1931) and Harvey (1987). Morphological terminology mostly follows Chamberlin (1931) and Harvey (1992).

The maps were produced with the computer program ArcView 3.2 after the relevant locality data were stored in an Access database. Coordinates were obtained from various sources, including the GeoNet Names Server (http://earth-info.nga.mil/gns/html/) produced by the National Geospatial-Intelligence Agency. Recently collected specimens were usually provided with GPS coordinates taken at the collecting site. The spellings of the Mexican place names follow Reddell (1981).

SYSTEMATICS

Family Ideoroncidae Chamberlin 1930

Pseudalbiorix Harvey, Barba, Muchmore & Pérez, new genus

Type species.—*Albiorix reddelli* Muchmore 1982.

Other species.—*Albiorix veracruzensis* Hoff 1945, *P. muchmorei* Barba & Pérez, new species and *P. armasi* Barba & Pérez, new species.

Etymology.—The name *Pseudalbiorix* refers to the morphological similarity that this genus bears to *Albiorix*. The gender is masculine, following the gender applied to the name *Albiorix* by Chamberlin (1930). Although not stated by Chamberlin (1930), the name was presumably derived from the Celtic god Albiorix, who was worshipped in ancient Gaul and is often thought to be equivalent to Teutates, and sometimes known as Caturix (Lindemans 2005).

Diagnosis.—*Pseudalbiorix* can be distinguished from all other ideoroncid genera by the enlarged and bifurcate condyle on the externo-distal margin of the chelal hand (Figs. 10, 31). In all other ideoroncid and, indeed, neobisioid genera (e.g., Figs. 4–7), this condyle is small and rounded.

Pseudalbiorix can be further separated from the other recognized genera of Ideoroncidae as follows: from the American genus *Albiorix* by the lack of a divided arolium; from the American genus *Ideoroncus* by the presence of 4 setae on the anterior margin of the carapace (6 setae in *Ideoroncus*) and the position of trichobothrium *st* which is situated slightly ventral to the level of *sb* in *Ideoroncus* but is not ventrally displaced in *Pseudalbiorix* (or any other ideoroncid); from the American genus *Typhloroncus* by the long arolium, the presence of eyes and by the slightly lower number of trichobothria (30 in *Pseudalbiorix* and 32 or 33 in *Typhloroncus*); from the Asian genera *Dhanus*, *Shravana* and *Nhatrangia* and the African genus *Negroroncus* by the absence of a lamina exterior [except in *D. siamensis* (With 1906) which will be transferred to a separate genus in a forthcoming review of the Asian Ideoroncidae]; and from the African genera *Nannoroncus* and *Afroroncus* by the lack of stout setae on the mesal surface of the chelal fingers.

Description.—*Adults:* All setae long, straight and acicular. Most cuticular surfaces smooth and glossy.

Pedipalps long and slender. Fixed chelal finger with 20 trichobothria, movable chelal finger with 10 trichobothria: *eb* region with 1 trichobothrium; *est* region with 6 trichobothria; *ib* region with 4 trichobothria; *ist* region with 5 trichobothria; *b* region with 2 trichobothria; and *t* region with 6 trichobothria; *st* not ventrally displaced. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and near *t* region in movable finger. Chelal teeth all closely spaced. Externodistal condyle on the chelal hand enlarged and bifurcate.

Chelicera with 6 or 7 long, acuminate setae on hand; movable finger with 1 long subdistal seta; flagellum of 4 thickened blades, all

blades serrate; lamina exterior absent; galea long and slender.

Cephalothorax: carapace with 2 small, bulging eyes; without furrows; anterior margin with 4 setae. Manducatory process with 2 long distal setae. Median maxillary lyrifissure present and sub-basally situated.

Abdomen: tergites and sternites undivided, but medial sternites with very thin medial suture line. Pleural membrane longitudinally striate. Each stigmatic sclerite with 1 or 2 setae. Spiracles simple, with spiracular helix.

Legs: femur I and II without basal swelling; femora I and II with primary slit sensillum directed transversely; femur I much longer than patella I; suture line between femur IV and patella IV transverse; metatarsus shorter than tarsus; metatarsal pseudotactile seta subproximal; legs with two bifid or trifid subterminal tarsal setae; arolium longer than claws, not divided but slightly indented at fringed ventral margin; claws slender and simple.

Nymphs: Much like adults, but trichobothrial patterns as follows: tritonymph with 14 on fixed finger and 8 on movable finger; deutonymph with 9 on fixed finger and 6 on movable finger; and protonymph with 3 on fixed finger and 1 on movable finger.

Remarks.—As discussed under the diagnosis, the principal feature by which species of *Pseudalbiorix* can be distinguished from all other ideoroncids is the presence of an enlarged and bifurcate externo-distal condyle on the chelal hand (Figs. 10, 31). This feature is found in all post-embryonic stages of *P. reddelli*, the tritonymphs of *P. veracruzensis* and *P. armasi*, and we presume that it also occurs in all other stages of members of the genus.

Apart from the two new species described herein, we also transfer two Mexican species, *A. veracruzensis* Hoff 1945 and *A. reddelli* Muchmore 1982, to *Pseudalbiorix*, as they possess all of the diagnostic features of the genus. Indeed, both Muchmore (1982) and Mahnert (1984) discussed the taxonomic position of *A. reddelli* and suggested that the species may be misplaced within *Albiorix*. With the discovery of additional species of similar morphology to *A. reddelli*, we here formally remove *A. veracruzensis* and *A. reddelli* from *Albiorix* and erect a new genus for this group of species.

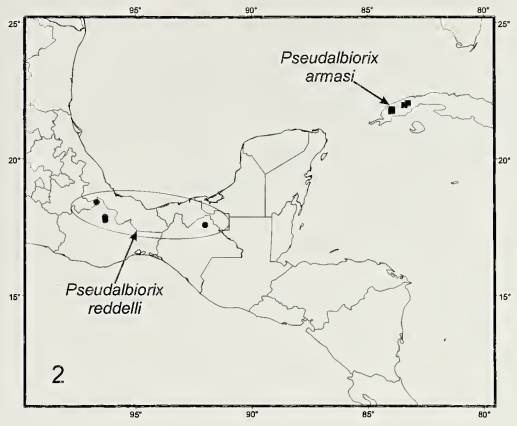
In a separate study, Harvey & Mahnert (2006) transferred the three Brazilian *Albiorix* species, *A. arboricola* (Mahnert 1979), *A. gracilis* Mahnert 1985 and *A. lamellifer* Mahnert 1985, to a separate genus *Xorilbia* Harvey & Mahnert 2006. The recognition of *Pseudalbiorix* and *Xorilbia* leaves *Albiorix* with just 11 species, distributed as follows: *A. anophthalmus* Muchmore 1999, *A. bolivari* Beier 1963, *A. conodentatus* Hoff 1945, *A. edentatus* Chamberlin 1930, *A. magnus* Hoff 1945, the type species *A. mexicanus* (Banks 1898), *A. mirabilis* Muchmore 1982, *A. parvidentatus* Chamberlin 1930, *A. retrodentatus* Hoff 1945 from Mexico or western USA, *A. argentiniensis* (Hoff 1950) from Argentina, and *A. chilensis* (Ellingsen 1905) from Chile. All species of the genus have deeply divided arolia, which are longer than the tarsi. Deeply divided arolia are not known in any other ideoroncid.

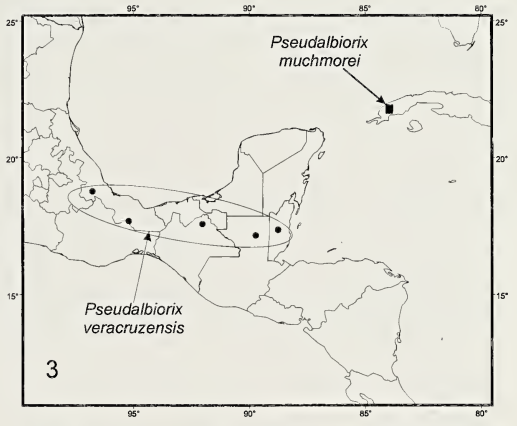
Distribution.—Members of the genus *Pseudalbiorix* have been recorded from Belize, Guatemala, southern Mexico and in western Cuba (Figs. 2, 3), in both cavernicolous and epigean habitats. Specimens have been mostly collected from habitats close to the ground such as litter, under stones or from logs, although two specimens of *P. veracruzensis* were taken from "under bark".

KEY TO SPECIES OF *PSEUDALBIORIX*

1. Most teeth of fixed chelal finger long and erect, clearly longer than wide 2
   Most teeth of fixed chelal finger of medium length and retrorse, clearly wider than long .. 3
2. Large troglomorphic species [e.g., pedipalpal femur 1.26–1.39 mm in length; chela (without pedicel) 2.10–2.24 mm in length] ..... *Pseudalbiorix muchmorei* (western Cuba)
   Medium-sized epigean species [e.g., pedipalpal femur 0.68–1.03 mm in length; chela (without pedicel) 1.14–1.68 mm in length] ..... *Pseudalbiorix armasi* (western Cuba)
3. Slightly larger in size [e.g., chela (with pedicel) length greater than 1.20 mm]; most teeth of fixed chelal finger triangular ..... *Pseudalbiorix reddelli* (Mexico)
   Slightly smaller in size [e.g., chela (with pedicel) length less than 1.20 mm]; most teeth of fixed chelal finger arcuate ..... *Pseudalbiorix veracruzensis* (Belize, Guatemala and Mexico)

Figure 1.—*Pseudalbiorix reddelli* (Muchmore), female from Cerro Cahui, Guatemala (FSCA, WM 8151).





Figures 2–3.—Maps showing known distributions of *Pseudalbiorix* species: 2. *P. reddelli* (Muchmore) and *P. armasi* Barba & Pérez, new species; 3. *P. veracruzensis* (Hoff) and *P. muchmorei* Barba & Pérez, new species.

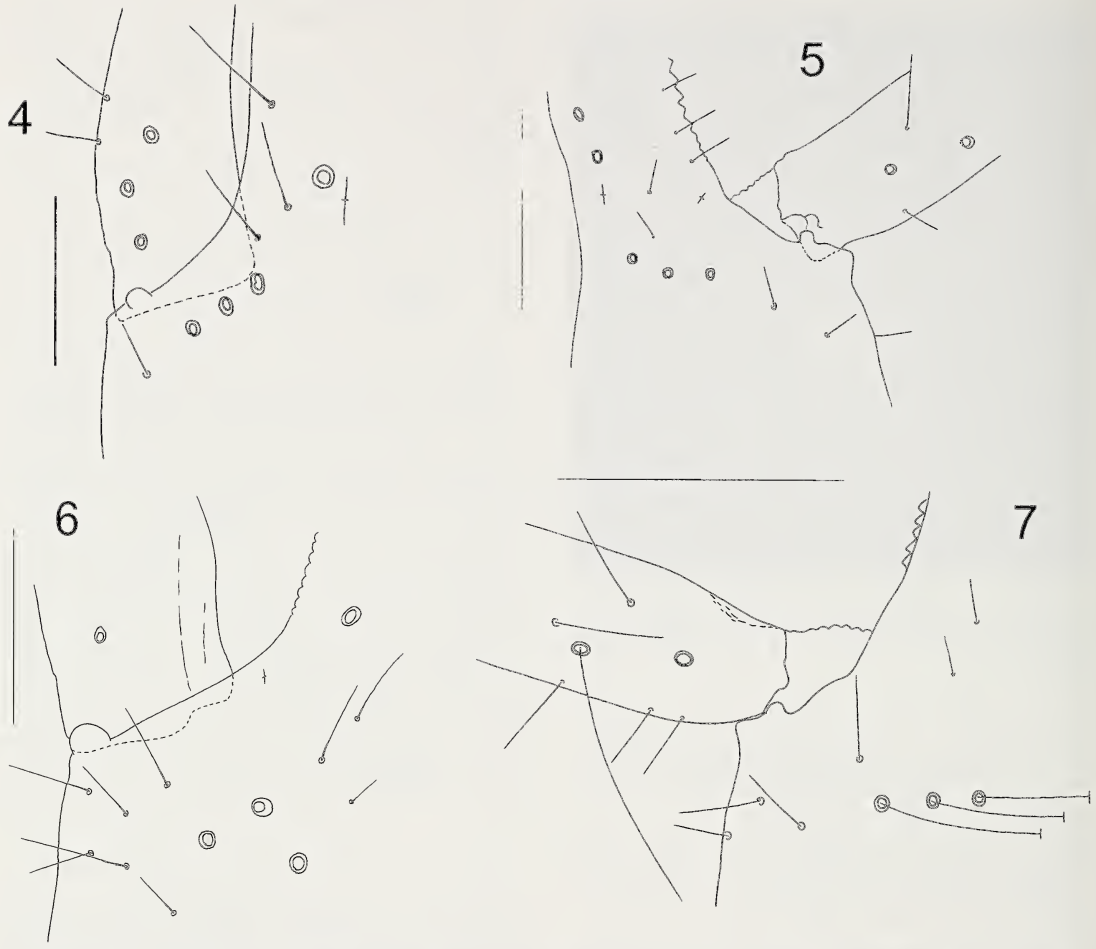
Pseudalbiorix reddelli (Muchmore 1982), NEW COMBINATION
Figs. 1, 2, 8–22

Albiorix reddelli Muchmore 1982:77, figs. 37–40; Mahnert 1984:676–677, fig. 47 (as *Albiorix* (?) *reddeli* [sic]); Harvey 1991:318.

Material examined.—MEXICO: *Oaxaca:* Holotype female, Grutas de Monteflor, 6 km N. of Valle Nacional [17°50′N, 96°19′W], 28 December 1972, J.R. Reddell (FSCA, WM 2957.01001, slide-mounted). Paratype: 1 female, same data as holotype (FSCA, WM 2957.01002, slide-mounted).

Other material: MEXICO: *Chiapas:* 1 ♂, 1 ♀, near Palenque, Chacamax R. road [17°29′N, 92°01′W], Berlese extraction from rotting log, 3 February 1976, C. Alteri (WAM T56705–56706, WM 4550.02001–2); 2 ♀, 1 tritonymph, 1 protonymph, Ruinas de Palenque [17°29′N, 92°01′W], litter, 29 March 1974, C. Alteri (FSCA, WM 3552.04001–4); 1 ♂, 1 ♀, La Canada, Palenque [17°29′N, 92°01′W], litter from woods, 27 March 1974, C. Alteri (FSCA, WM 3546.03002); 1 protonymph, Palenque Ruins [17°29′N, 92°01′W], 16 March 1975, C. Alteri (FSCA, WM 3977.02001); 1 deutonymph, Olvidado, Ruinas de Palenque [17°29′N, 92°01′W], under stone, March 1983, C. Alteri (FSCA, WM 6391.01001); *Oaxaca:* 1 ♂, Cueva de la Culebra, 10 km SW. of Acatlán de Perez Figueroa [18°28′N, 96°41′W], 7 December 1993, P. Sprouse (FSCA, WM 7974.02001); 1 ♂, 1 ♀, 6 miles [= 9.7 km] S. of Valle Nacional [17°41′N, 96°19′W], 2000 feet [= 608 m], 19 May 1971, S. Peck (FSCA, WM 2522.03001–2).

Diagnosis.—*Pseudalbiorix reddelli* differs from the Cuban species *P. muchmorei* and *P. armasi* by the shape of the fixed chelal finger teeth which are long and erect in the two Cuban species, but short and retrorse in *P. reddelli*. It differs from *P. veracruzensis* by the shape of the fixed chelal finger teeth which are arcuate in *P. veracruzensis*, but are mostly triangular without arcuate edges in *P. reddelli*. They also differ in size, as *P. reddelli* is



Figures 4–7.—Detail of chelal externo-distal condyle: 4. *Ideoroncus lenkoi* Beier, male from São Sebastiao, Station Biologique, São Paulo, Brazil (WAM 90/1166); 5. *Albiorix mirabilis* Muchmore 1982, holotype male from Cueva de las Maravillas, Oaxaca, Mexico (FSCA, WM 4675.03001); 6. *Dhanus sumatranus* (Redikorzev 1922), male from 'Datu Caves, Sumatra' (CAS, JC-103.01001); 7. *Typhloroncus coralensis* Muchmore 1979, male from St John, U.S. Virgin Islands (FSCA, WM 6566.02001). Scale lines = 0.05 mm (Fig. 4), 0.2 mm (Figs. 5–7).

slightly larger than *P. veracruzensis* [e.g., the chela (with pedicel) measurements taken are depicted in Fig. 8].

Description.—*Adult:* Color light red-brown. Setae long, straight and acicular.

Pedipalp (Fig. 11): femur lightly granulate on anterior margin, trochanter and patella with scattered granulations; trochanter 1.79–2.22 (♂), 1.95–2.22 (♀), femur 3.68–3.79 (♂), 3.40–3.96 (♀), patella 2.52–2.84 (♂), 2.55–3.00 (♀), chela (with pedicel) 3.69–4.03 (♂), 3.42–4.12 (♀), chela (without pedicel) 3.61–3.87 (♂), 3.38–3.95 (♀), hand 1.64–1.80 (♂), 1.49–1.73 (♀) times longer than broad, movable finger 1.17–1.26 (♂), 1.11–1.31 (♀) times longer than hand. Fixed chelal finger with 20 trichobothria, movable chelal finger with 10 trichobothria (Fig. 17): *eb, esb* and *isb* in straight row at base of finger; *eb, esb, isb, it* and *et* regions each with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 5 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and near

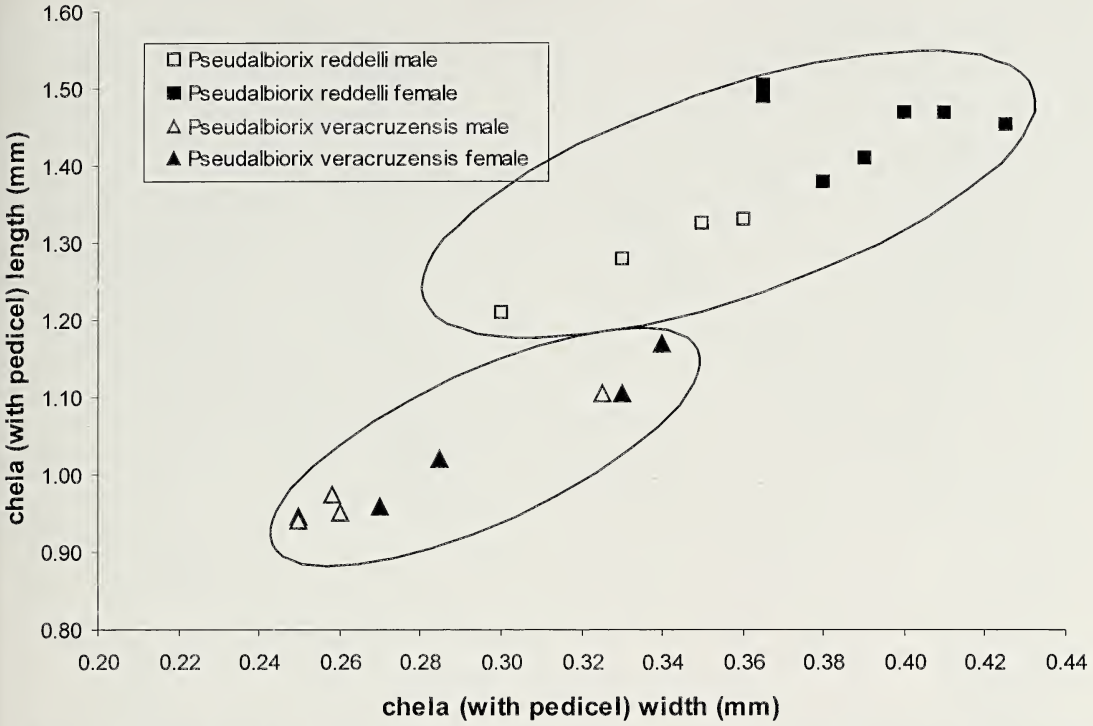


Figure 8.—Graph depicting pedipalpal chela (with pedicel) length versus width in *Pseudalbiorix reddelli* and *P. veracruzensis*. Females are depicted with closed symbols and males with open symbols.

basal section of *t* region in movable finger. Chelal hand with externo-distal condyle enlarged and bifurcate (Fig. 10). Chelal teeth evenly spaced: fixed finger with 32–37 (♂, ♀) slightly retrorse teeth, margins triangular, not arcuate; movable finger with 21–25 (♂, ♀) low, rounded teeth, plus two small upraised distal teeth.

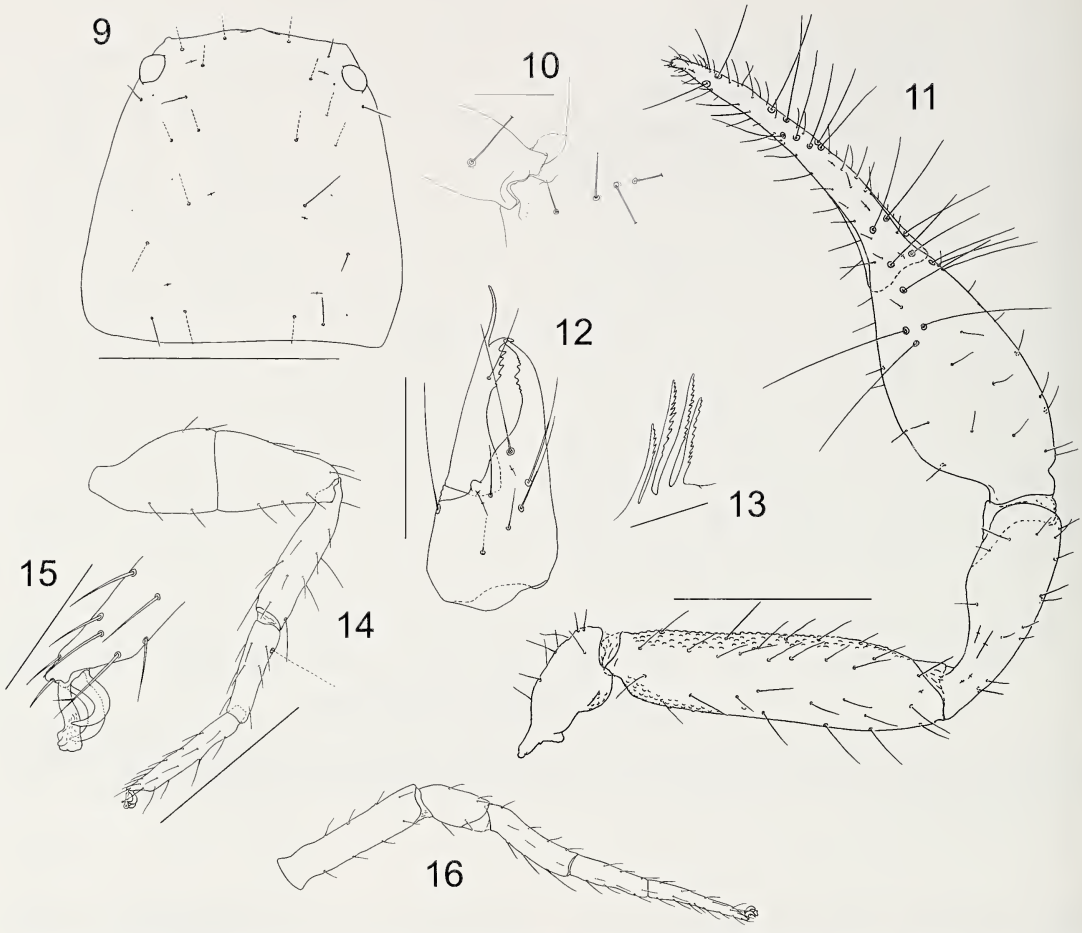
Chelicera (Fig. 12): with 6 or, very occasionally, 7 setae on hand [7 on left chelicera of holotype]; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 5–6 (♂, ♀) small teeth as well as several minute teeth; movable finger with 5–6 (♂, ♀) teeth; flagellum (Fig. 13) of 4 blades, each with several serrations; lamina exterior absent.

Cephalothorax: carapace (Fig. 9) 0.94–1.11 (♂), 0.97–1.00 (♀) times longer than broad; lateral margins evenly convex; with 2 small bulging eyes; with small epistome; with ca. 22 setae, including 4 setae on anterior margin and 4 on posterior margin; without furrows. Coxal chaetotaxy: ♂ (WM 2522.03002), 3: 5: 5: 5; holotype ♀, 5: 5: 5: 5; pedipalpal coxa with 2 apical setae, apex somewhat pointed.

Abdomen: tergites not divided, medial sternites with very thin medial suture line; sclerites uniseriate. Tergal chaetotaxy: ♂ (WM 2522.03002), 2: 4: 6: 8: 9: 11 10: 9: 9: 9 (including 2 tactile setae): 7: 2; holotype ♀, 2: 4: 5: 7: 9: 10: 9: 9: 10: 8: 7: 2. Sternal chaetotaxy: ♂ (WM 2522.03002), 6: (2)2[4](2): (2)6(2): 11: 12: 12: 12: 11: 11: 9: 2; holotype ♀, 6: (2)3(2): (2)4(2): 10: 9: 11: 11: 11: 12: 8: 2; setae of anterior genital operculum (sternite II) of ♀ very small. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia of male with small dorsal apodeme, median genital sac not preserved in material examined; genitalia of female with large gonosac which is covered with scattered pores.

Legs (Figs. 14–16): femur+patella 2.56–2.82 (♂), 2.21–2.98 (♀) times longer than broad; subterminal tarsal setae trifurcate; arolium longer than claws, not divided.



Figures 9–16.—*Pseudalbiorix reddelli* (Muchmore), holotype female, unless stated otherwise: 9. Carapace; 10. Detail of left chelal externo-distal condyle; 11. Right pedipalp, dorsal view; 12. Left chelicera; 13. Left flagellum, female from 6 miles [= 9.7 km] S. of Valle Nacional (FSCA, WM 2522.03001); 14. Left leg IV; 15. Detail of distal end of tarsus IV; 16. Left leg I. Scale lines = 0.5 mm (Figs. 9, 11, 14, 16), 0.2 mm (Fig. 12), 0.1 mm (Figs. 10, 13, 15).

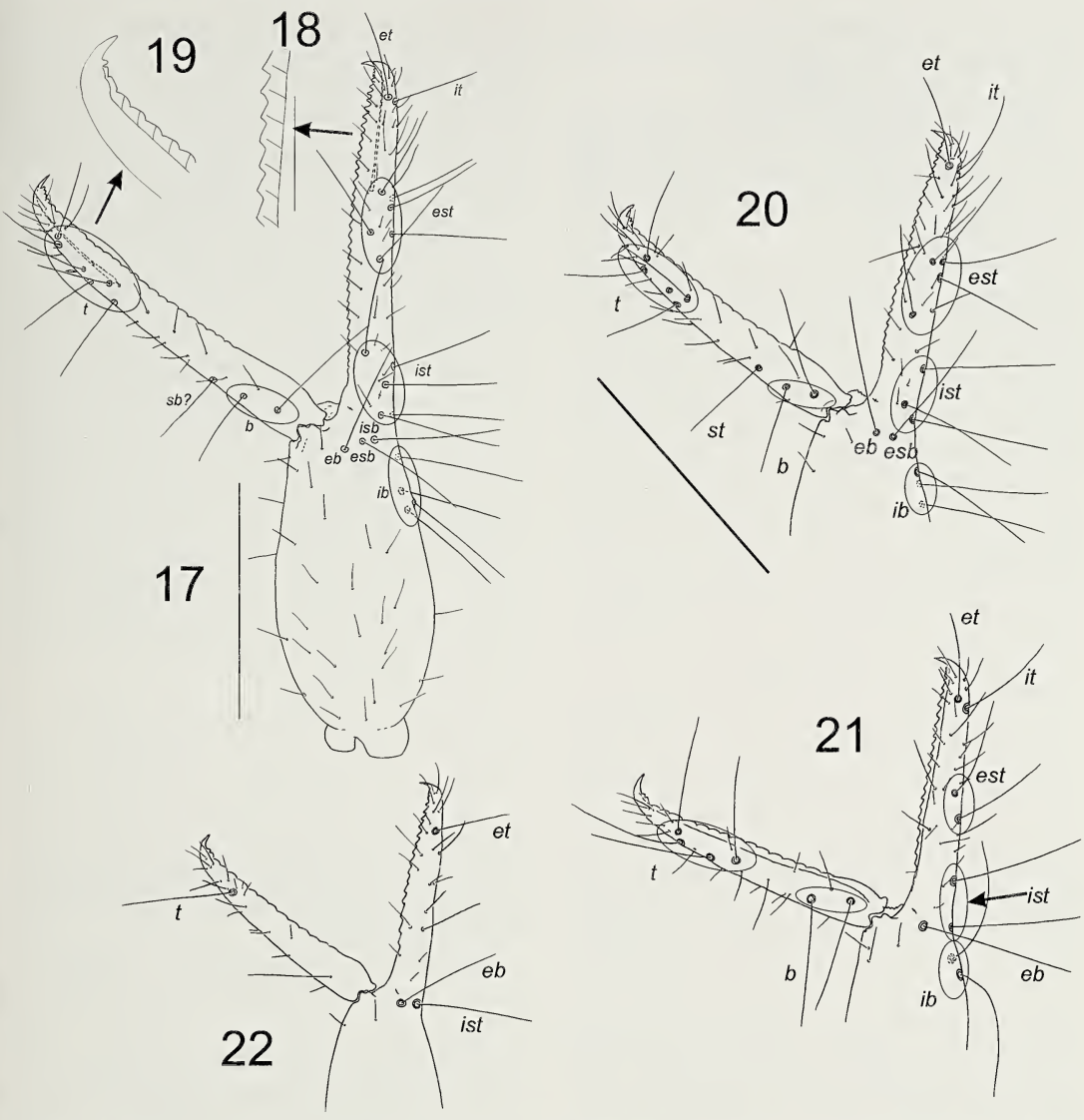
Tritonymph: Pedipalps: trochanter 1.97, femur 3.41, patella 2.31, chela (with pedicel) 3.68, chela (without pedicel) 3.57 times longer than broad. Fixed finger with 14 trichobothria, movable finger with 8 trichobothria (Fig. 20); *eb, esb, it* and *et* regions each with 1 trichobothrium; *ib* region with 3 trichobothria; *ist* region with 3 trichobothria; *est* region with 4 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *st* region with 1 trichobothrium; *t* region with 5 trichobothria. Chelal hand with externo-distal condyle enlarged and bifurcate.

Chelicera: galea long, nearly straight; hand with 5 setae, movable finger with 1 seta; fixed finger with 5 small teeth, movable finger with 5 small teeth; flagellum composed of 4 blades, all serrate.

Cephalothorax: carapace: small epistome present; one pair of small eyes present; with 4 setae on anterior margin and 4 setae on posterior margin.

Legs: metatarsus and tarsus not fused; arolium longer than claws, not divided.

Deutonymph: Pedipalps: trochanter 2.09, femur 3.71, patella 2.32, chela (with pedicel) 3.95, chela (without pedicel) 3.86 times longer than broad. Fixed finger with 9 trichobothria, movable finger with 6 trichobothria (Fig. 21); *eb, it* and *et* regions each with 1 trichobothrium; *ib* region with 3 trichobothria; *ist* region with 1 trichobothrium; *est* region with 2 tri-



Figures 17–22.—*Pseudalbiorix reddelli* (Muchmore), holotype female, unless stated otherwise: 17. Left chela, lateral view; 18. Detail of teeth from fixed finger; 19. Detail of teeth from moveable finger; 20. Left chela, lateral view, tritonymph from Ruinas de Palenque (FSCA, WM 3552.04003); 21. Left chela, lateral view, deutonymph from Ruinas de Palenque (FSCA, WM 6391.01001); 22. Left chela, lateral view, protonymph from Ruinas de Palenque (FSCA, WM 3552.04004); Scale lines = 0.5 mm (Figs. 17, 20–22), 0.1 mm (Figs. 18, 19).

chobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *t* region with 4 trichobothria. Chelal hand with externo-distal condyle enlarged and bifurcate.

Chelicera: galea long, slightly curved; hand with 5 setae, movable finger with 1 seta; fixed finger with 6 small teeth, movable finger with 5 small teeth; flagellum composed of 4 blades, all serrate.

Cephalothorax: carapace 0.98 times longer than broad; small epistome present; one pair of small eyes present; with 4 setae on anterior margin and 4 setae on posterior margin.

Legs: metatarsus and tarsus not fused; arolium longer than claws, not divided.

Protonymph: Pedipalps: trochanter 1.73–1.89, femur 3.36–3.50, patella 2.17–2.23, chela (with pedicel) 3.74–4.13, chela (without pedicel) 3.66–4.06 times longer than broad. Fixed finger with 3 trichobothria, movable fin-

ger with 1 trichobothrium (Fig. 22); *eb, et, ist* and *t* present. Chelal hand with externo-distal condyle enlarged and bifurcate.

Chelicera: galea long, nearly straight; hand with 4 setae, movable finger without seta; fixed finger with 4 small teeth, movable finger with 3 small teeth; flagellum composed of 4 blades, all serrate.

Cephalothorax: carapace 1.03 times longer than broad; very small epistome present; one pair of small eyes present; with 4 setae on anterior margin and 2 setae on posterior margin. Posterior maxillary lyrifissure absent.

Legs: metatarsus and tarsus not fused; arolium longer than claws, not divided.

Dimensions (mm).—*Males:* specimen from 6 miles [= 9.7 km] S. of Valle Nacional (from near type locality) (WM 2522.03002) followed by other males: Body length 2.17 (1.97–2.01). Pedipalps: trochanter 0.355/0.16 (0.325–0.35/0.155–0.19), femur 0.77/0.205 (0.72–0.81/0.19–0.22), patella 0.54/0.19 (0.48–0.56/0.185–0.21), chela (with pedicel) 1.28/0.33 (1.21–1.33/0.30–0.36), chela (without pedicel) 1.235 (1.16–1.30), hand length 0.57 (0.54–0.59), movable finger length 0.665 (0.65–0.74). Chelicera 0.325/0.15 (0.2950.33/0.15–0.18). Carapace 0.65/0.665 (0.635–0.65/0.57–0.69); eye diameter 0.07 (0.06–0.064). Leg I: femur 0.38/0.105 (0.38–0.40/0.105–0.11), patella 0.19/0.10 (0.18–0.19/0.095–0.11), tibia 0.265–0.075 (0.245–0.25/0.07–0.075), metatarsus 0.18/0.06 (0.17/0.06–0.07), tarsus 0.28/0.045 (0.25–0.29/0.04–0.06). Leg IV: femur + patella 0.62/0.22 (0.58–0.64/0.22–0.25), tibia 0.415/0.105 (0.39–0.42/0.095–0.10), metatarsus 0.25/0.075 (0.235–0.25/0.075–0.08), tarsus 0.36/0.05 (0.32/0.37/0.05).

Females: Holotype FSCA (WM 2957.01001) followed by other females: Body length 2.53 (1.95–2.63). Pedipalps: trochanter 0.37/0.18 (0.37–0.40/0.17–0.19), femur 0.90/0.23 (0.83–0.87/0.22–0.25), patella 0.614/0.205 (0.56–0.61/0.19–0.23), chela (with pedicel) 1.504/0.365 (1.38–1.49/0.37–0.43), chela (without pedicel) 1.440 (1.35–1.44), hand length 0.629 (0.63–0.68), movable finger length 0.819 (0.75–0.83). Chelicera 0.333/0.154 (0.36–0.39/0.16–0.19). Carapace 0.640/0.688 (0.65–0.71/0.70–0.72); eye diameter 0.064 (0.06–0.07). Leg I: femur 0.447/0.109 (0.42–0.45/0.11–0.125), patella 0.211/0.103 (0.21–0.22/0.11–0.115), tibia 0.294/0.074 (0.245–0.295/0.08–0.085), metatarsus 0.218/0.061 (0.18–0.215/0.065–0.075), tarsus 0.294/0.045 (0.28–0.31/0.05). Leg IV: femur + patella 0.706/0.237 (0.64–0.71/0.245–0.29), tibia 0.464/0.100 (0.41–0.46/0.10–0.12), metatarsus 0.289/0.077 (0.25–0.30/0.08–0.09), tarsus 0.371/0.058 (0.295–0.39/0.055–0.06).

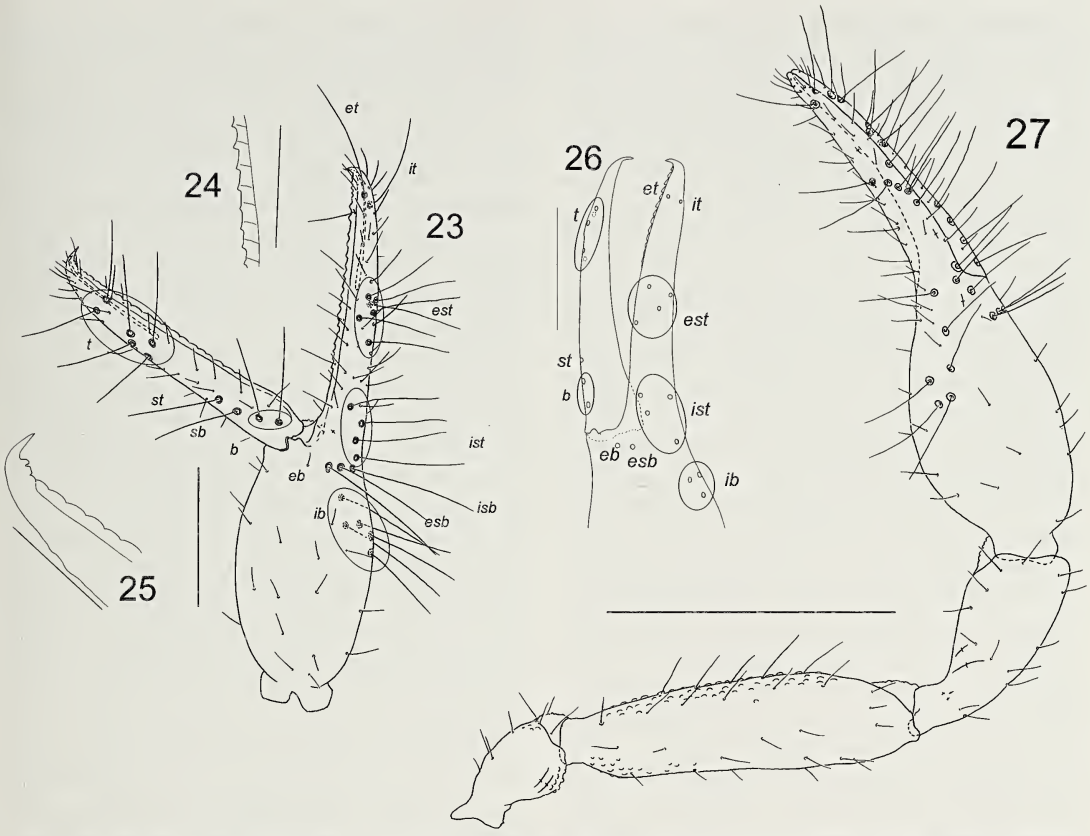
Tritonymph: Specimen from Ruinas de Palenque (WM 3552.04003): Body length 1.95. Pedipalps: trochanter 0.295/0.150, femur 0.630/0.185, patella 0.415/0.180, chela (with pedicel) 1.105/0.300, chela (without pedicel) 1.070, hand length (without pedicel) 0.490, movable finger length 0.590. Carapace 0.550/?.

Deutonymph: Specimen from Olvidado, Ruinas de Palenque (WM 6391.01001): Body length 1.440. Pedipalps: trochanter 0.230/0.110, femur 0.520/0.140, patella 0.325/0.140, chela (with pedicel) 0.87/0.220, chela (without pedicel) 0.850, hand length (without pedicel) 0.380, movable finger length 0.490. Carapace 0.480/0.49.

Protonymph: Specimen from Ruinas de Palenque (FSCA, WM 3552.04004): Body length 1.10. Pedipalps: trochanter 0.190/0.110, femur 0.420/0.125, patella 0.260/0.120, chela (with pedicel) 0.71/0.190, chela (without pedicel) 0.695, hand length (without pedicel) 0.295, movable finger length 0.400. Carapace 0.360/0.350.

Remarks.—*Pseudalbiorix reddelli* is known from the southern Mexican states of Chiapas and Oaxaca (Fig. 2), where it occurs in litter, under stones, in rotting logs and inside caves. The two type specimens from Grutas de Monteflor possess a slightly more slender chela than the other specimens which, apart from a single male specimen taken from a cave (Cueva de la Culebra, Oaxaca), were collected from epigean habitats. We can find no other substantial differences between any of the cave-dwelling specimens and their epigean counterparts and conclude that they all represent a single species.

At Palenque (Chiapas), *P. reddelli* occurs sympatrically with *P. veracruzensis* (Figs. 2, 3), but it appears that they may be separated ecologically, as most records of *P. reddelli* appear to be from ground habitats (under stones, in litter, inside logs), whereas *P. veracruzensis* was found "under bark", presumably of a tree.



Figures 23–27.—*Pseudalbiorix veracruzensis* (Hoff), male from 2.5 km S. of Belmopan, Belize (FSCA, WM 3067.03001), unless stated otherwise: 23. Left chela, lateral view; 24. Detail of teeth from fixed finger; 25. Detail of teeth from moveable finger. 26. Left chela, dorsolateral view, setae omitted, paratype tritonymph (AMNH); 27. Right pedipalp, dorsal view. Scale lines = 0.5 mm (Fig. 27), 0.25 (Fig. 23), 0.2 mm (Fig. 26), 0.1 mm (Figs. 24, 25).

Pseudalbiorix veracruzensis (Hoff 1945), NEW COMBINATION
Figs. 3, 8, 23–27

Albiorix veracruzensis Hoff 1945:4–7, figs 6–9; Harvey 1991:318.

Material examined.—MEXICO: *Veracruz-Llave:* Paratypes: 2 males, 1 tritonymph, "Buena Ventura" plantation [ca. 17°37′N, 95°12′W], July 1909, A. Petrunkevitch (AMNH, slide-mounted).

Other material: BELIZE: *Cayo:* 2 ♂, 1 ♀, 2.5 miles [= 4.0 km] S. of Belmopan [17°14′N, 88°46′W], 4 August 1972, berlese, limestone forest, S. and J. Peck (FSCA, WM 3067.03001–3); 2 ♂, 1 ♀, Belmopan [17°15′S, 88°46′W], 1–15 August 1972, berlese, termite nests, S. and J. Peck (WAM T56707–56709, WM 3066.05001–3). GUATEMALA: *Petén:* 1 ♀, biotopo Cerro Cahui [17°00′N, 89°44′W], 18 April 1996, S. Foia (FSCA, WM 8151). MEXICO: *Chiapas:* 1 ♂, 1 ♀, Palenque [17°29′N, 92°01′W], under bark, 23 January 1976, C. Alteri (FSCA, WM 4537.01001–2); *Veracruz-Llave:* 1 ♀, Atoyac [18°54′N, 96°46′W], "bosque", 13 November 1941, C. Bolívar, F. Bonet (CAS, JC-1888.01001).

Diagnosis.—*Pseudalbiorix veracruzensis* differs from all other members of the genus by its small size [e.g., chela (with pedicel) length 0.94–1.105 (♂), 0.96–1.17 (♀) mm] and by the shape of the teeth of the fixed chelal finger which have an arcuate outline. It is most similar to *P. reddelli* but is slightly smaller [e.g., the chela (with pedicel) measurements taken are depicted in Fig. 8].

Description.—*Adult:* Color light red-brown. Setae long, straight and acicular.

Pedipalp (Fig. 27): femur lightly granulate

on anterior and postero-basal margins, trochanter and patella with scattered granulations; trochanter 2.04–2.24 (♂), 2.00–2.19 (♀), femur 3.41–3.78 (♂), 3.46–3.76 (♀), patella 2.41–2.59 (♂), 2.45–2.63 (♀), chela (with pedicel) 3.40–3.90 (♂), 3.35–3.58 (♀), chela (without pedicel) 3.32–3.70 (♂), 3.32–3.47 (♀), hand 1.60–1.74 (♂), 1.56–1.72 (♀) times longer than broad, movable finger 1.11–1.18 (♂), 1.05–1.14 (♀) times longer than hand. Fixed chelal finger with 20 trichobothria, movable chelal finger with 10 trichobothria (Fig. 23): *eb, esb* and *isb* in straight row at base of finger; *eb, esb, isb, it* and *et* regions each with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 5 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and near basal section of *t* region in movable finger. Chelal hand with externo-distal condyle enlarged and bifurcate. Chelal teeth evenly spaced: fixed finger (Fig. 24) with 23–26 (♂, ♀) strongly retrorse teeth, most with arcuate margins; movable finger (Fig. 25) with 18–23 (♂, ♀) low, rounded teeth, plus two small upraised distal teeth.

Chelicera: with 6 setae on hand; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 4–5 (♂, ♀) small teeth as well as several minute teeth; movable finger with 5–6 (♂, ♀) teeth; flagellum of 4 blades, each with several serrations; lamina exterior absent.

Cephalothorax: carapace 0.99–1.38 (♂), 0.98–1.15 (♀) times longer than broad; lateral margins evenly convex; with 2 small bulging eyes; with small epistome; with ca. 22 setae, with 4 setae on anterior margin and 4 on posterior margin; without furrows. Coxal chaetotaxy: ♂ (WM 3067.03001), 4: 4: 5: 6; ♀ (WM 3067.03003), 4: 5: 5: 6; pedipalpal coxa with 2 apical setae, apex somewhat pointed.

Abdomen: tergites not divided, medial sternites with very thin medial suture line; sclerites uniseriate. Tergal chaetotaxy: ♂ (WM 3067.03001), 2: 4: 7: 8: 9: 9: 9: 8: 9: 9: 5: 2; ♀ (WM 3067.03003), 2: 3: 8: 8: 8: 9: 9: 9: 9: 7: 4: 2. Sternal chaetotaxy: ♂ (WM 3067.03001), 9: (1)6[6](1): (2)3(2): 8: 9: 9: 10: 11: 11: 7: 2; ♀ (WM 3067.03003), 5: (1)2(1): (2)2(2): 10: 9: 10: 9: 11: 11: 4: 2. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia of male with small dorsal apodeme, median genital sac not preserved in material examined; genitalia of female with large gonosac that is covered with scattered pores.

Legs: femur + patella 2.30–2.43 (♂), 2.48–2.66 (♀) times longer than broad; subterminal tarsal setae trifurcate; arolium longer than claws, not divided.

Tritonymph: Pedipalps: trochanter 2.06, femur 3.57, patella 2.30, chela (with pedicel) 3.65, chela (without pedicel) 3.48 times longer than broad. Fixed finger with 15 trichobothria, movable finger with 8 trichobothria (Fig. 26); *eb, esb, it* and *et* regions each with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 3 trichobothria; *est* region with 4 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *st* region with 1 trichobothrium; *t* region with 5 trichobothria. Chelal hand with externo-distal condyle enlarged and bifurcate.

Chelicera: galea long, slightly curved; hand with 6 setae, movable finger with 1 seta; fixed and moveable fingers each with 5 small teeth; flagellum composed of 4 blades, all serrate.

Cephalothorax: carapace: small epistome present; one pair of small eyes present; with 4 setae on anterior margin and 4 setae on posterior margin.

Legs: metatarsus and tarsus not fused; arolium longer than claws, not divided.

Dimensions (mm).—*Males:* Specimen from 2.5 miles [= 4.0 km] S. of Belmopan, Belize (FSCA, WM 3067.03001) followed by other males, including paratypes: Body length 1.89 (1.81–1.95). Pedipalps: trochanter 0.28/0.125 (0.265–0.30/0.13–0.14), femur 0.64/0.17 (0.60–0.665/0.160–0.195), patella 0.415/0.16 (0.385–0.445/0.16–0.185), chela (with pedicel) 0.975/0.258 (0.942–1.105), chela (without pedicel) 0.94 (0.925–1.08), hand length 0.45 (0.42–0.52), movable finger length 0.53 (0.495–0.58). Chelicera 0.26/0.125 (0.25–0.30/0.12–0.155). Carapace 0.585/0.52 (0.53–0.615/0.385–0.62); eye diameter 0.05 (0.055–0.065). Leg I: femur 0.32/0.095 (0.30–0.35/0.085–0.11), patella 0.16/0.09 (0.15–0.18/0.085–0.105), tibia 0.20/0.065 (0.19–0.22/0.065–0.075), metatarsus 0.155/0.05 (0.13–0.155/0.05–0.06), tarsus 0.23/0.045 (0.23/0.045). Leg IV: femur + patella 0.51/

0.22 (0.49–0.57), tibia 0.34/0.09 (0.31–0.36/0.090.105), metatarsus 0.215/0.065 (0.18–0.23/0.0650.075), tarsus 0.29/0.045 (0.265–0.295/0.0450.05).

Females: Specimen from 2.5 miles [= 4.0 km] S. of Belmopan, Belize (FSCA, WM 3067.03003) followed by other females: Body length 2.24 (1.55–2.41). Pedipalps: trochanter 0.295/0.135 (0.31–0.33/0.155–0.16), femur 0.64/0.17 (0.59–0.725/0.16–0.20), patella 0.42/0.16 (0.39–0.465/0.15–0.19), chela (with pedicel) 1.02/0.285 (0.96–1.17/0.27–0.34), chela (without pedicel) 0.99 (0.905–1.14), hand length 0.49 (0.42–0.555), movable finger length 0.54 (0.48–0.585). Chelicera 0.29/0.14 (0.26–0.32/0.13–0.16). Carapace 0.58/0.59 (0.47–0.63/0.41–0.70); eye diameter 0.05 (0.05–0.06). Leg I: femur 0.32/0.095 (0.36/0.11), patella 0.16/0.085 (0.18/0.105), tibia 0.21/0.065 (0.215–0.22/0.075), metatarsus 0.155/0.05 (0.15–0.155/0.055–0.06), tarsus 0.22/0.045 (0.22–0.23/0.045–0.05). Leg IV: femur + patella 0.52/0.21 (0.55–0.585/0.22), tibia 0.34/0.09 (0.37–0.385/0.095–0.10), metatarsus 0.22/0.065 (0.20–0.23/0.07–0.075), tarsus 0.295/0.05 (0.29–0.295/0.05–0.055).

Tritonymph: Paratype from La Buena Ventura, Veracruz-Llave (AMNH): Body length 1.52. Pedipalps: trochanter 0.237/0.115, femur 0.486/0.136, patella 0.320/0.139, chela (with pedicel) 0.829/0.227, chela (without pedicel) 0.790, hand length (without pedicel) 0.368, movable finger length 0.442. Carapace 0.450/0.365.

Remarks.—The type locality of *Albiorix veracruzensis*, "La Buena Ventura," was a rubber plantation situated in the southern region of Veracruz-Llave, on the border of Oaxaca situated amongst tropical rainforest (Petrunkevitch 1909). Although we were unable to locate and examine the holotype of *A. veracruzensis*, the three paratypes confirm the identity of this species.

Pseudalbiorix veracruzensis is known from Belize, Guatemala and the southern Mexican states of Chiapas and Veracruz-Llave (Fig. 3). The specimens from Belize were taken in Berlese samples in limestone forest and termite nests, the pair from Chiapas was collected from under bark and the female from Atoyac was taken from forest. All specimens are of a small size and possess the characteristically shaped teeth on the fixed chelal finger. As discussed under *P. reddelli*, at Palenque (Chiapas), *P. reddelli* occurs sympatrically (Figs. 2, 3) with *P. veracruzensis* but it appears that they may be separated ecologically.

Pseudalbiorix muchmorei Barba & Pérez, new species
Figs. 3, 28–32

New genus, new species A: Barba & Pérez 2001: 24.

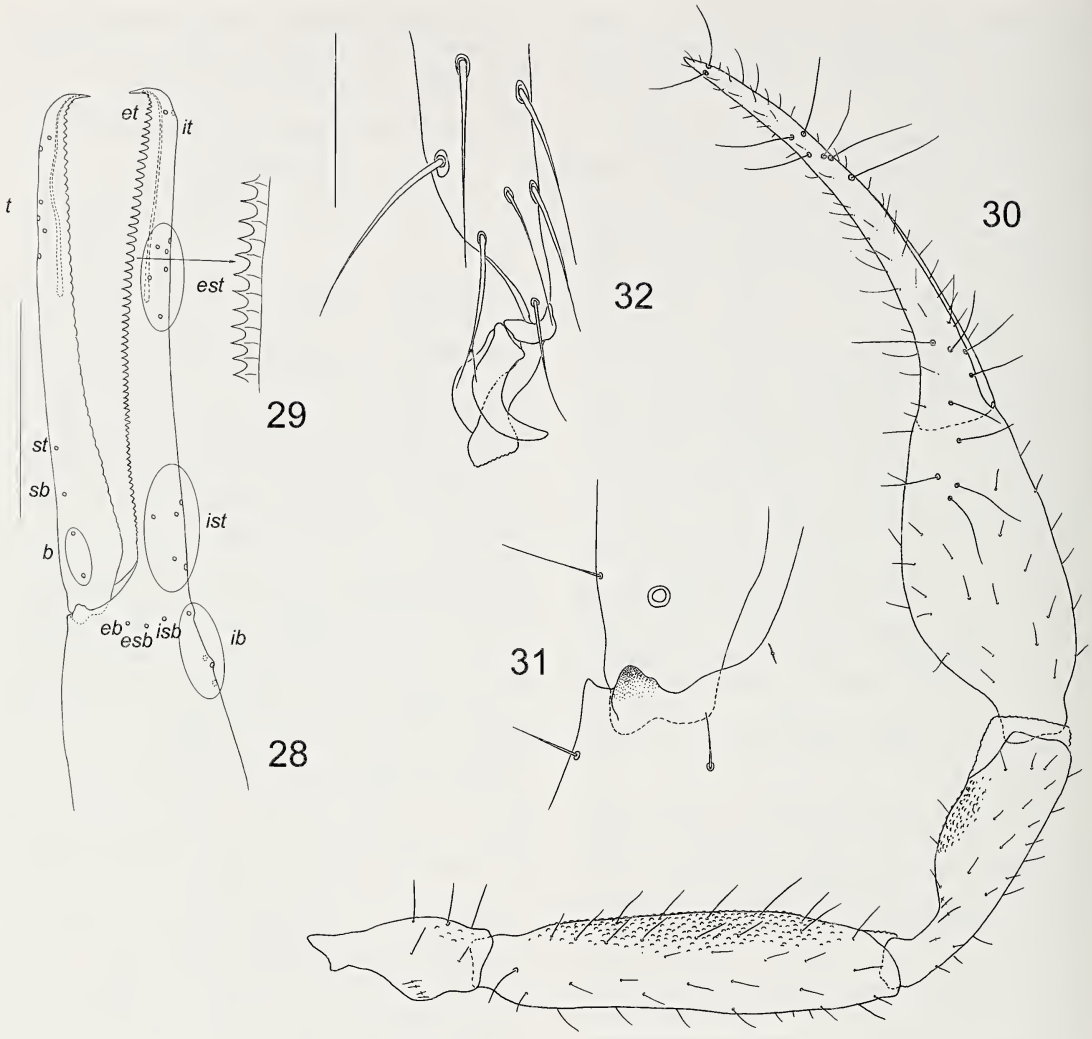
Material examined.—CUBA: *Pinar del Río Province:* Holotype male, Cueva de los Murciélagos, La Jíquima, Gramales, Minas de Matahambre [22°27′56″N, 83°57′47″W], 11 August 1997, R. Barba (ColBK). Paratypes: CUBA: *Pinar del Río Province:* 2 females, same data as holotype (ColBK); 1 female, same data as holotype, except 19 February 1997, no collector (ColBK); 1 female, from the entrance of Cueva de la Majagua, Luis Lazo [22°22′34″N, 83°58′16″W], 11 February 1979, L.F. Armas (CZACC); 1 male, 1 female, Cueva de las Dos Anas, Sistema Subterraneo de Majaguas-Cantera, Sierra de San Carlos, Guane [22°22′34″N, 83°58′16″W], 13 October 1990, A. Pérez (WAM T56393).

Etymology.—This species is named in honor of our co-author W.B. Muchmore, whose research into American pseudoscorpions has forged a new era in our understanding of these fascinating arachnids.

Diagnosis.—Troglobitic species with pale coloration and elongate appendages; large size, 2.92–3.40 mm in length. Pedipalps very long, pedipalpal chela (without pedicel) 2.10–2.24 mm in length. Movable finger with 40–45 marginal teeth, distal ones conical with cusps well developed, the proximal ones much flattened.

Description.—*Adult:* Carapace and palps light brown, other parts pale. Setae long, straight and acicular.

Pedipalp (Fig. 30): very long: femur and patella medially granulated, trochanter with small granules, other surfaces smooth; trochanter 2.06–2.54, femur 3.32–5.31, patella 2.33–3.23, chela (without pedicel) 4.00–4.56, hand 1.92–2.14 times longer than deep, movable finger 1.38–1.44 times longer than hand. Fixed chelal finger with 20 trichobothria, movable chelal finger with 10 trichobothria (Fig. 28): *eb, esb* and *isb* in straight row at base of finger; *eb, esb, isb, it* and *et* regions each with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 5 trichobothria;



Figures 28–32.—*Pseudalbiorix muchmorei* Barba & Pérez, new species, paratype male from Cueva de las Dos Anas (WAM T56393): 28. Left chela, lateral view, setae omitted; 29. Detail of teeth from fixed finger; 30. Right pedipalp, dorsal view; 31. Detail of left chelal externo-distal condyle; 32. Detail of distal end of right tarsus IV. Scale lines = 0.5 mm (Figs. 28, 30), 0.05 mm (Fig. 32).

est region with 6 trichobothria; *et* opposite *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and near basal section of *t* region in movable finger. Chelal hand with externo-distal condyle enlarged and slightly bifurcate (Fig. 31). Chelal teeth evenly spaced: fixed finger (Fig. 29) with 54–55 large, long, acutely conical teeth; movable finger with 40–45 teeth, more conical distally and more rounded basally.

Chelicera: with 7 setae on hand; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 5–6 small teeth; movable finger with 5–6 teeth; flagellum of 4 blades, each with several serrations; lamina exterior absent.

Cephalothorax: carapace longer than broad; lateral margins evenly convex; surface reticulated; with 2 small bulging eyes; with small epistome; with ca. 32 setae, including 4 setae on anterior margin and 4 on posterior margin; without furrows. Pedipalpal coxa with 2 apical setae, apex somewhat pointed.

Abdomen: tergites not divided, anterior ter-

gites finely reticulated; sternites IV–IX with very thin medial suture line; sclerites uniseriate. Tergal chaetotaxy: ♂, 2: 2: 4: 6: 7: 8: 8: 8: 9: 4: 8: 2; ♀, 2: 2: 4: 6: 6: 6: 5: 7: 6: 6:?: 2. Sternal chaetotaxy: ♂, 9: (1)9[3 + 3](1): (2)5(2): 7: 7: 10: 9: 9: 8: 2; ♀, 8: (2)2(2): (2)5(2): 9: 8: 8: 9: 9: 10:? : 2; setae of anterior genital operculum (sternite II) of ♀ small. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia of male with small dorsal apodeme, median genital sac not visible in material examined; genitalia of female with large gonosac which is covered with scattered pores.

Legs: leg I with femur 2.13–4.57 times as long as patella; femur + patella 2.40–2.76 times longer than broad; tibia 4.71–5.67 times longer than deep; subterminal tarsal setae trifurcate on legs I and II, and bifid on legs III and IV; metatarsus IV with single subproximal tactile seta; arolium longer than claws, not divided but slightly indented at middle and with distal ventral margins fringed.

Dimensions (mm).—*Male (holotype):* Body length 3.00. Carapace length 0.94. Chelicera 0.44/0.20. Pedipalps: trochanter 0.56/0.24, femur 1.26/0.38, patella 0.84/0.36, chela (without pedicel) 2.16/0.50, hand (without pedicel) 0.92/0.46, pedicel length 0.06, movable finger length 1.32. Leg I: femur 0.62/0.12, patella 0.28/0.12, tibia 0.46/0.08, metatarsus 0.28/0.06, tarsus 0.36/0.04. Leg IV: femur + patella 0.96/0.40, tibia 0.62/0.12, metatarsus 0.34/0.08, tarsus 0.54/0.06.

Female (4 paratypes): Body length 2.92–3.40. Carapace length 0.94–0.96. Chelicera 0.44–0.56/0.18–0.22. Pedipalps: trochanter 0.54–0.56/0.22–0.26, femur 1.26–1.39/0.26–0.38, patella 0.80–0.90/0.26–0.36, chela (without pedicel) 2.10–2.24/0.46–0.54, hand (without pedicel) 0.90–1.04/0.42–0.50, pedicel length 0.06–0.10, movable finger length 1.30–1.46. Leg I: femur 0.62–0.68/0.12–0.14, patella 0.26–0.32/0.12, tibia 0.42–0.46/0.08, metatarsus 0.28–0.32/0.06–0.07, tarsus 0.34–0.41/0.04–0.05. Leg IV: femur+patella 0.96–1.04/0.37–0.40, tibia 0.62–0.68/0.12–0.14, metatarsus 0.33–0.38/0.08–0.10, tarsus 0.50–0.54/0.06–0.07.

Variation.—The holotype possesses a teratological flagellum on the left chelicera, which bears five subequal serrate blades.

Remarks.—*Pseudalbiorix muchmorei* is very similar to *P. armasi*, both found in western Cuba, but differs by its clear troglomorphic characteristics. Although not presenting anophthalmy, *P. muchmorei* shows other troglomorphic characters such as pale coloration, large body size and elongated appendages, particularly the pedipalps with very long fingers and more marginal teeth in the movable finger (40–45 in *P. muchmorei* and 26–28 in *P. armasi*).

The specimens were collected under stones in the twilight and dark zones of caves located within the Sierra de los Órganos, Pinar del Río Province, western Cuba (Fig. 3). *Pseudalbiorix muchmorei* is the third troglobitic pseudoscorpion species to be reported from Cuba, the others are *Antillobisium mitchelli* Dumitresco & Orghidan and *A. vachoni* Dumitresco & Orghidan (Dumitresco & Orghidan 1977).

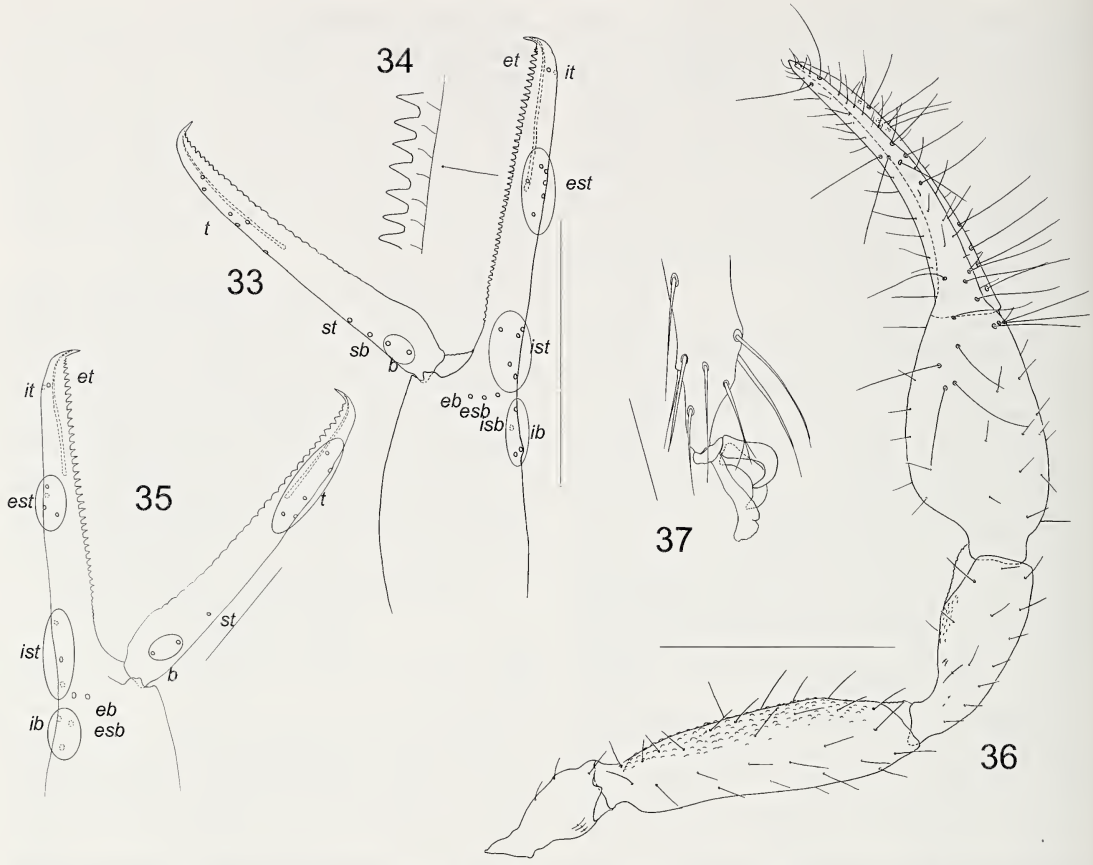
Pseudalbiorix armasi Barba & Pérez, new species
Figs. 2, 33–37

New genus, new species B: Barba & Pérez 2001: 24.

Material examined.—CUBA: *Pinar del Río Province:* Holotype male, Parque la Güira, San Diego de los Baños [22°38′37″N, 83°25′24″W], January 1985, L.F. Armas (CZACC). Paratypes: CUBA: *Pinar del Río Province:* 2 females, same data as holotype (CZACC); 1 male, 1 female, Sierra de San Carlos, Luis Lazo [22°22′20″N, 83°59′03″W], February 1979, L.F. Armas (CZACC); 1 male, 1 female, Loma "El Toro", San Cristóbal [22°43′26″N, 83°16′36″W], 15 February 1981, L.F. Armas (CZACC); 1 female, entrance of Cueva de los Santos Cuajaní, Sierra del Rosario, San Cristóbal [coordinates unknown], 19 February 1981, L.F. Armas (CZACC); 1 male, mogote La Jíquima, Gramales, Minas de Matahambre [22°27′56″N, 83°57′47″W], 23 July 1997, N. Torres, A. Pérez González (ColBK); 2 males, 2 females, same data except 25 February 2001, R. Barba (WAM T56394); 3 males, 1 tritonymph, Luis Lazo, Sabana Llana [22°25′13″N, 83°57′33″W], 29 May 1974, G. Alayon (FSCA, WM 4513.01001–4).

Etymology.—This species is named in honor of Dr L.F. Armas, collector of part of the type series, for his contribution to Central American arachnology.

Diagnosis.—Epigean species smaller than *P. muchmorei*, 1.82–2.63 mm in length. Ped-



Figures 33–37.—*Pseudalbiorix armasi* Barba & Pérez, new species, paratype male from Luis Lazo (FSCA, WM 4513.01001), unless stated otherwise: 33. Left chela, lateral view, setae omitted; 34. Detail of teeth from fixed finger; 35. Right chela, lateral view, tritonymph from Luis Lazo (FSCA, WM 4513.01004); 36. Right pedipalp, dorsal view; 37. Detail of distal end of left tarsus IV. Scale lines = 0.2 mm (Fig. 35), 0.5 mm (Figs. 31, 36), 0.05 mm (Fig. 37).

ipalps with chela (without pedicel) 1.14–1.68 mm long. Movable finger of pedipalpal chela with 26–28 short marginal teeth, distal ones rounded without cusps, proximal ones much flattened.

Description.—*Adult:* Carapace and palps dark brown, other parts much lighter. Setae long, straight and acicular.

Pedipalp (Fig. 36): femur medially granulated, trochanter and patella with small granules, other surfaces smooth; trochanter 1.84–2.32, femur 3.43–4.45, patella 2.50–2.97, chela (without pedicel) 3.47–4.20, hand 1.56–2.00 times longer than deep, movable finger 1.24–1.44 times longer than hand. Fixed chelal finger with 20 trichobothria, movable chelal finger with 10 trichobothria (Fig. 33): *eb, esb* and *isb* in straight row at base of finger; *eb, esb, isb, it* and *et* regions each with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 5 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and near basal section of *t* region in movable finger. Chelal hand with externo-distal condyle enlarged and slightly bifurcate. Chelal teeth evenly spaced: fixed finger (Fig. 34) with 46–47 large, long, acutely conical teeth; movable finger with 26–28 teeth, rounded distally and more flattened basally.

Chelicera: with 7 setae on hand; movable finger with 1 subdistal seta; galea very slender

and elongate; fingers with 4–8 small teeth; flagellum of 4 blades, each with several serrations; lamina exterior absent.

Cephalothorax: carapace longer than broad; lateral margins evenly convex; surface reticulated; with 2 small bulging eyes; with small epistome; with ca. 29 setae, including 4 setae on anterior margin and 4 on posterior margin; without furrows. Pedipalpal coxa with 2 apical setae, apex somewhat pointed.

Abdomen: tergites not divided, anterior tergites finely reticulated, others smooth; sternites III–VIII with very thin medial suture line; sclerites uniseriate. Tergal chaetotaxy: holotype ♂, 2: 2: 6: 6: 9: 9–10: 9–10: 9–10: 12: 8–9: 8–9: 2; paratype ♀: 2: 4: 5: 5: 6: 8: 8: 8: 8:? :? : 2. Sternal chaetotaxy: holotype ♂, 10: (1)8[3+3](1): (2)8(2): 11: 11: 13: 14: 13: 15:? : 2; paratype ♀: 9:? : (2)4(2): 8: 10: 10: 10: 12: 12:? : 2.; setae of anterior genital operculum (sternite II) of ♀ small. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia of male with small dorsal apodeme, median genital sac not visible in material examined; genitalia of female with large gonosac which is covered with scattered pores.

Legs: leg I with femur 2.0–2.25 times longer than patella; femur+patella 1.58–2.60 times longer than broad; tibia 3.60–4.60 times longer than deep; subterminal tarsal setae trifurcate on legs I and II, and bifid on legs III and IV; metatarsus IV with single subproximal tactile seta; arolium longer than claws (Fig. 37), not divided but slightly indented at middle and with distal ventral margins fringed.

Tritonymph: Pedipalps: trochanter 2.02, femur 3.37, patella 2.56, chela (with pedicel) 3.87, chela (without pedicel) 3.72 times longer than broad. Fixed finger with 14 trichobothria, movable finger with 8 trichobothria (Fig. 35); *eb, esb, it* and *et* regions each with 1 trichobothrium; *ib* region with 3 trichobothria; *ist* region with 3 trichobothria; *est* region with 4 trichobothria; *et* adjacent to *it*; *b* region with 2 trichobothria; *st* region with 1 trichobothrium; *t* region with 5 trichobothria. Chelal hand with externo-distal condyle enlarged and bifurcate.

Chelicera: galea long, slightly curved; hand with 6 setae, movable finger with 1 seta; fixed finger with 3 small teeth and moveable finger with 5 small teeth; flagellum composed of 4 blades, all serrate.

Cephalothorax: carapace: very small epistome present; one pair of small eyes present; with 4 setae on anterior margin and 2 setae on posterior margin.

Legs: metatarsus and tarsus not fused; arolium longer than claws, not divided.

Dimensions (mm).—holotype male, followed by 8 paratypes. Body length 2.04 (1.82–2.63). Carapace length 0.64 (0.62–0.76). Chelicera 0.30/0.14 (0.29–0.40/0.14–0.20). Pedipalps: trochanter 0.34/0.17 (0.32–0.44/0.14–0.20), femur 0.88/0.20 (0.68–1.03/0.18–0.24), patella 0.50/0.20 (0.48–0.64/0.18–0.23), chela (without pedicel) 1.28/0.32 (1.14–1.68/0.30–0.42), hand (without pedicel) 0.54/0.30 (0.50–0.74/0.27–0.40), pedicel length 0.06 (0.06–0.08), movable finger length 0.78 (0.72–1.06). Leg I: femur 0.36/0.10 (0.33–0.48/0.10–0.12), patella 0.16/0.09 (0.16–0.22/0.09–0.11), tibia 0.24/0.06 (0.22–0.30/0.06–0.08), metatarsus 0.18/0.06 (0.15–0.24/0.04–0.06), tarsus 0.27/0.04 (0.23–0.31/0.04–0.05). Leg IV: femur+patella 0.60/0.38 (0.56–0.78/0.28–0.38), tibia 0.36/0.10 (0.36–0.48/0.10–0.12), metatarsus 0.21/0.09 (0.18–0.30/0.06–0.08), tarsus 0.33/0.04 (0.30–0.40/0.04–0.06).

Tritonymph: Paratype from Luis Lazo (FSCA, WM 4513.01004: Body length 1.74. Pedipalps: trochanter 0.269/0.133, femur 0.576/0.171, patella 0.389/0.152, chela (with pedicel) 1.033/0.267, chela (without pedicel) 0.992, hand length (without pedicel) 0.442, movable finger length 0.570. Carapace 0.531/0.461.

Remarks.—This species is known from Sierra de los Órganos and Sierra del Rosario, Pinar del Río Province, Cuba (Fig. 2), where it has been collected from under stones in evergreen forests.

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MECHANICAL ENERGY OSCILLATIONS DURING LOCOMOTION IN THE HARVESTMAN *LEIOBUNUM VITTATUM* (OPILIONES)

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ABSTRACT. The long legs, compact body and hanging posture of many harvestmen are unique among terrestrial animals, but no quantitative analyses of locomotion have been conducted to determine if this extreme morphology is associated with novel mechanisms of locomotion. Here we have undertaken a three-dimensional kinematic analysis of running *Leiobunum vittatum* (Say 1821) using field-by-field analysis of high-speed video. The center of mass of harvestmen was found to undergo vertical and transverse displacements of unprecedented magnitude, but the pattern of displacements was consistent with those predicted by general models of energetic efficiency and dynamic stability of pedestrian locomotion. Because these models assume substantial roles for elastic energy storage in leg elements, elasticity is probably an important component of the locomotor mechanism in harvestmen, and we identify two skeletomuscular elements as possible springs.

Keywords: Kinematics, elastic mechanisms, running, leg springs

Many harvestmen have exceptionally long legs, compact bodies and an ability to move rapidly on structurally complex horizontal and vertical surfaces. Yet, the kinematics of these common and familiar animals has never been described quantitatively let alone compared to that of more well-studied arthropods and vertebrates. Here we describe locomotion of a common "daddy longlegs," *Leiobunum vittatum* (Say 1821), by examining the three-dimensional kinematics of animals running on a smooth, horizontal surface. We conclude that harvestmen use the same basic locomotor mechanisms as other pedestrian animals, although their unusual morphology significantly amplifies the sinusoidal vertical and transverse displacements of the body during locomotion. Specifically, we find that forward kinetic energy fluctuates in phase with potential energy as predicted by the spring-loaded inverted-pendulum model, which maintains that elastic energy is stored at one phase of the step cycle and converted to kinetic energy in a subsequent phase (Cavagna et al. 1977; Heglund et al. 1982; Alexander 1984, 1988; McMahon 1985, 1990; Farley et al. 1993; Full & Farley 2000). We also observe that fluctuations in forward velocity of the center of mass occur at roughly twice the frequency of fluctuations in the transverse (lateral) velocity, a pattern consistent with that predicted by the lateral leg-spring model, which invokes elastic leg elements as a mechanism of passive (non-reflex) stabilization (Kubow & Full 1999; Schmidt & Holmes 2000a, b; Schmidt et al. 2002). These findings suggest that the legs of harvestmen act as springs in both the vertical and transverse axes that provide energetic efficiency and stability, respectively.

METHODS

Kinematics.—*Leiobunum vittatum* (n = 6 males, mass 50 ± 3 mg) (all values are mean ± SE unless otherwise noted) were captured in a wooded area in College Park, Maryland, USA in August 2002 and were used in experiments within 24 h. Voucher specimens were deposited in the Denver Museum of Nature & Science, Denver, CO. Animals were induced to run on a smooth non-slip horizontal surface in the laboratory. They ran using stride frequencies between 3.6–5.2 Hz for several seconds when disturbed but favored lower speeds at other times. Images of fast-running

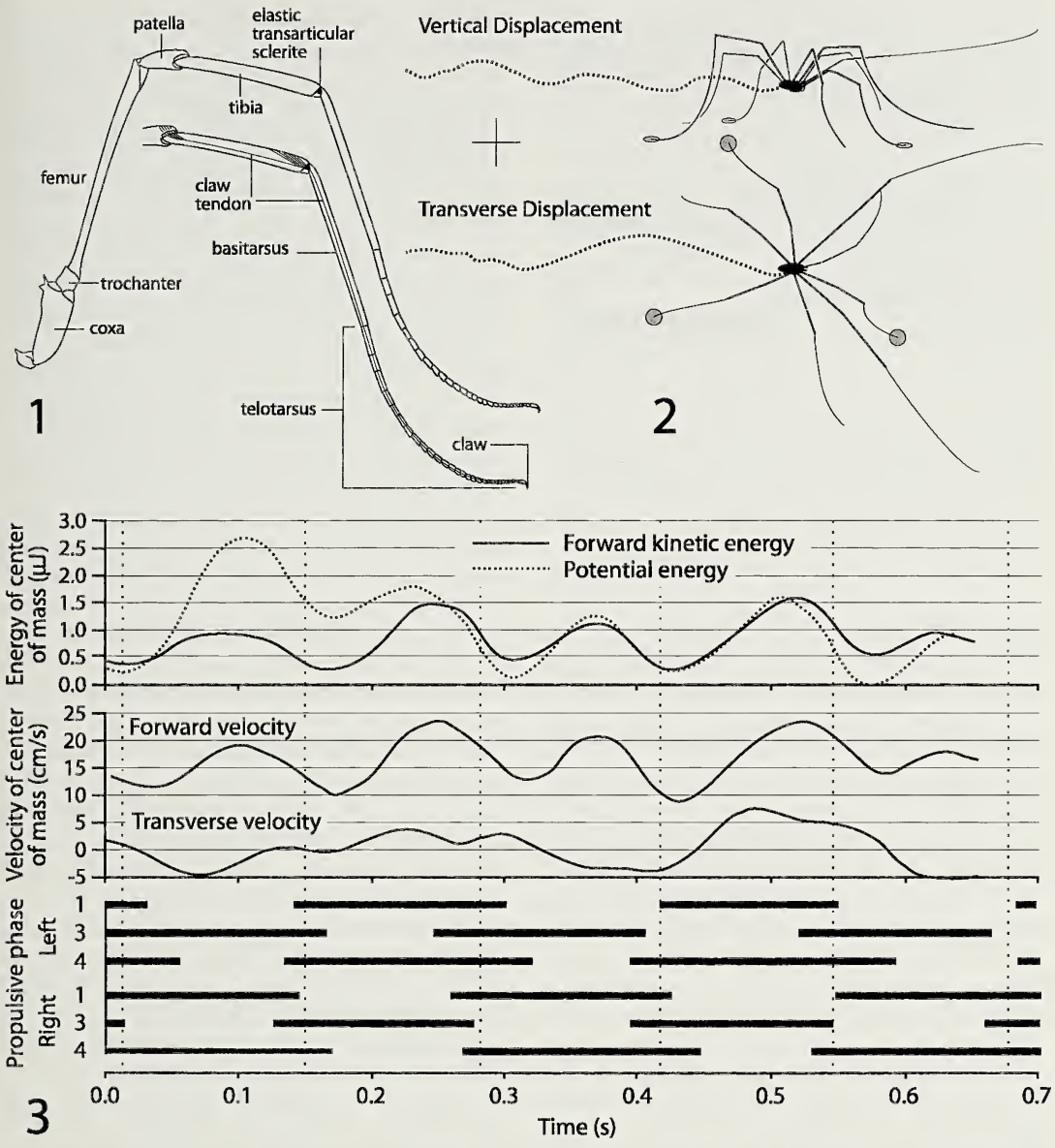
animals were captured using two synchronized (gen-locked) Peak Performance video cameras (120 fields/s) positioned to obtain lateral and dorsal perspectives. The angle between the cameras was about 90°. Videotapes were synchronized using a Peak Performance manually operated event marker. A calibration frame (4 cm × 4 cm × 4 cm) was videotaped by both cameras and filled most of the two fields of view. The frame consisted of 12 noncoplanar points. The resolution of points of the calibration frame was about 0.2 mm. Points in space could be located with mean-squared errors of 0.12 mm, 0.26 mm, and 0.15 mm for the x, y, and z positions, respectively, yielding a 0.32 mm mean-squared error for position.

Videotapes were analyzed using a computerized motion analysis system (Motus, Peak Performance Technologies, Inc., version 6.0). The field of view was such that about two complete strides of each animal were captured during a run. A sequence was analyzed only if it was not interrupted by pauses or obvious changes in speed. The center of the body, distal end of the tarsus, tibia-tarsus joint, and femur-patella joint (Fig. 1) were digitized manually. Data from both cameras were treated using a low-pass, fourth-order, zero-phase-shift Butterworth digital filter with a cutoff-frequency of 10 Hz (Biewener & Full 1992) before direct linear transformation to three-dimensional coordinates. The overall animal center of mass was calculated for each field and incorporated the body and the center of mass of each effective leg segment.

Mechanical energy.—Masses of the body and effective leg segments were obtained by freezing specimens at 0° C for 30 min. Because the patella was short and essentially immobile relative to the tibia, the patella and tibia were treated together as one effective leg segment. Each leg was severed at the tibia-tarsus, femur-patella, and coxa-trochanter joints and each effective leg segment was weighed to the nearest μg (ATI-CAHN C-33 balance). Estimates of mechanical energy were derived from kinematic and mass measurements (Kram et al. 1997). The body constituted 73.0 ± 0.8% of total mass. When leg segments were taken into account, the overall center of mass was indistinguishable from the center of the body, except in the vertical axis, where the center of mass was located 0.5–2.0 mm above the body. The center of the body was considered a sufficiently close approximation of the overall center of mass for use in calculations. Potential energy of the center of mass was calculated as mgh, where m was animal mass, g was gravitational acceleration, and h was height of the center of mass relative to the substratum. Forward kinetic energy of the center of mass was calculated as $\frac{1}{2}mv^2$ where v was velocity of the body. Total mechanical energy is the sum of kinetic and potential energy. Translational kinetic energies of the effective segments of leg 4 was calculated as $\frac{1}{2}mv^2$, where m was the mass of the effective leg segment and v was the velocity of the center of mass of the effective segment relative to the body. The rotational kinetic energy of each effective leg segment was calculated as $\frac{1}{2}I\omega^2$, where I was the inertia of the effective segment about its center of mass and ω was the angular velocity of that segment in a global coordinate system. The moment of inertia for each effective segment was approximated by $(^1/_{12})ml^2$, where l was the length of the segment, which assumed each segment to be a slender rod of uniform density. Total limb kinetic energy was estimated by summing the translational and rotational energy fluctuations of the segments of leg 4 during a stride and multiplying by eight the total number of legs. This estimate was justified due to the similar shape and mass of the eight legs.

RESULTS

Kinematics.—Like other phalangid harvestmen, *Leiobunum vittatum* behaved as a functional hexapod, the antenniform second legs being used primarily as tactile organs. They used a hexapod–like alternating tripod gait, which provides a stable base of support throughout the locomotor cycle (Delcomyn 1985). Specifically, legs left 1, right 3 and left 4 moved essentially together as one tripod and moved out of phase with the tripod formed by legs right 1, left 3 and right 4 (Figs. 2, 3). At the onset of a step cycle, legs of one tripod contacted the substratum and members of the other tripod were lifted. At this point, the center of mass moved to its lowest level of 10 ± 0.4 mm or 1.7 ± 0.2 body lengths above the substratum. Retraction of leg 4 of a supporting tripod began at 16 ± 1% of the stride period before the lowest position of the center of mass was reached (Fig. 4). The center of mass



Figures 1–3.—1. Semi-diagrammatic retrolateral (posterior) view of the first leg of *Leiobunum vittatum* showing basic anatomy and locations of possible spring-like mechanisms. 2. Body trajectory of a harvestman running at an approximate net speed of 17 cm/s from dorsal and lateral perspectives. Highlighted leg tips indicate the tripod of support. Scale bars = 1 cm. 3. An example of changes in kinetic and potential energy and in forward and transverse velocity in a harvestman running at an approximate net speed of 17 cm/s. The upper graph shows that forward kinetic and gravitational potential energy of the center of mass fluctuate in phase, as predicted by the spring-loaded inverted-pendulum model. The middle graph shows fluctuations in forward and transverse velocity of the center of mass. Note that negative velocities indicate transverse velocities when the center of mass is left of the net axis of travel and positive values are used when the center of mass is on the right. The pattern is roughly consistent with predictions of the lateral-leg-spring (LLS) hypothesis. The lower graph shows the stepping pattern (alternating tripod gait), with periods of support indicated by dark bars. Vertical dotted lines indicate the approximate point at which one tripod of support shifts to the other.

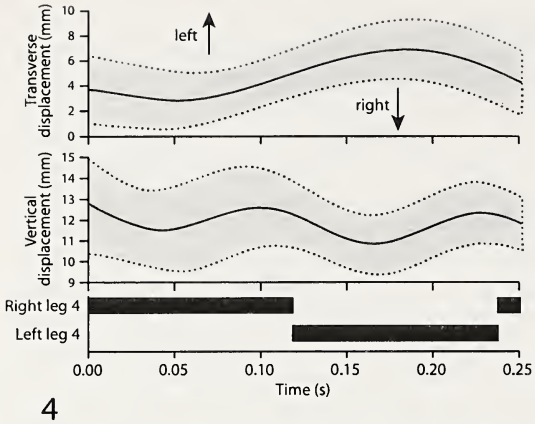


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Figure 4.—Average and SD of the center of mass position of running harvestman. Displacement over 1 stride from four individuals was normalized to step period (Motus, Peak Performance Technologies, Inc., version 6.0).

then moved upward to 13 ± 0.4 mm (2.2 ± 0.2 body lengths) as leg 4 of the supporting tripod appeared to push the body over the set of "crutches" formed by legs 1 and 3. Significantly, the plane of extension of leg 4 was not parallel to the overall axis of travel, and the center of mass was displaced transversely toward the side opposite the extending leg by 4.7 ± 0.4 mm (0.8 ± 0.2 body lengths). This mechanism resulted in a lurching motion with instantaneous forward velocity of the center of mass varying almost sinusoidally from 15–25 cm/s when the animal ran at an average speed of 20 cm/s (30.3 body lengths/s) (Figs. 2, 3).

Mechanical energy.—Forward kinetic and potential energy of the center of mass changed approximately in phase, with the average phase difference being less than the video time resolution. Vertical excursion of the center of mass in *L. vittatum* spanned slightly less than one body length, such that changes in potential energy (1.1 ± 0.10 μJ) were about twice that of the corresponding changes in kinetic energy (0.7 ± 0.06 μJ). Individual legs were 2.8–4.2% of total body mass. The kinetic energy associated with stopping and starting leg 4 during a stride was 0.020–0.025 μJ, with about 14% of this energy due to rotation of the segments. Assuming that kinetic energy of all legs was similar to leg 4 at observed running velocities, the magnitude of the limb kinetic energy oscillations was 9–15% of the mechanical energy oscillations of the center of mass.

DISCUSSION

Significance of vertical fluctuations of the center of mass.—Comparative studies of legged locomotion in arthropods and vertebrates have revealed patterns of movement that transcend leg number, body size and phylogenetic distance (Full & Koditschek 1999; Blickhan & Full 1993; Farley et al. 1993; Full & Farley 2000). Cyclical changes in the vertical position of the body's center of mass is one such pattern and is hypothesized to increase overall energetic efficiency through the interchange of kinetic and gravitational potential energy. The inverted pendulum (IP) model (Cavanga et al. 1977) applies to an animal moving forward while vaulting over a stiffened leg, as exemplified by a person using a pair of crutches. In the initial part of the step cycle, some kinetic energy used in moving the animal forward also raises the center of mass and increases gravitational potential energy. As the center of mass falls, potential energy is converted into kinetic energy, some of which can be used in initiating the next step cycle. The IP model predicts that changes in potential and forward kinetic energy occur 180° out of phase. Significantly, behavior consistent with the IP model has never been observed in arthropods and was not observed in *L. vittatum*.

In the spring-loaded inverted-pendulum (SLIP) model (Cavagna et al. 1977; Heglund et al. 1982; Alexander 1984, 1988; McMahon 1985, 1990; Farley et al. 1993; Full & Farley 2000), elastic elements in the legs serve as mechanisms of transient energy storage. Specifically, as the center of mass descends under the force of gravity elastic elements in the legs (that is, tensed muscles, tendons, and skeletal structures) are deformed, and forces produced by subsequent elastic recoil of these elements are used to propel the center of mass upward and forward to initiate a new cycle. In contrast to the IP model, the SLIP model predicts that forward kinetic and gravitational potential energy fluctuate in phase. The SLIP model matches locomotion in many vertebrates (Biewener et al. 1981; Alexander 1984; Farley et al. 1993), crabs (Blickhan & Full 1987), and cockroaches (Full & Tu 1990). Our observations of *L. vittatum* were also consistent with the SLIP model, and this species is the

least massive animal in which the predictions of the model have been met.

Significance of transverse displacements in the center of mass.—The magnitude of the transverse displacements of the center of mass observed in running *L. vittatum* (peak-to-peak displacement of 0.78 body lengths) (Figs. 2–4) are unprecedented. By comparison, the center of mass of the cockroach *Blaberus discoidalis* deviates laterally from the net axis of travel by less than 0.4 mm or 0.01 body lengths (Full & Tu 1990). The existence of substantial transverse accelerations of the body would seem to be energetically inefficient (Manton 1977) in the absence of a mechanism analogous to the SLIP model. Recent work suggests that cyclical transverse displacements are associated with a passive spring-based mechanism of directional stabilization that can respond to external perturbations to forward locomotion more rapidly than reflexes (Kubow & Full 1999; Schmidt & Holmes 2000a, b; Schmidt et al. 2002). Specifically, when a running animal experiences a transverse perturbation to the center of mass (wind, uneven substratum, another animal, etc.), leg springs could potentially absorb the energy and thereby prevent significant deviation from the net axis of travel. Some of this stored energy could also be converted to transverse kinetic energy upon elastic recoil and stored transiently by elastic elements in the legs on the opposite side of the animal. Theoretically, it is possible that energy from a brief transverse perturbation could be dissipated by elastic mechanisms over several strides while the center of mass oscillates along the net axis of travel.

The lateral-leg-spring model (LLS) of stabilization makes specific predictions about the timing of forward and transverse fluctuations of the center of mass (Kubow & Full 1999; Schmidt & Holmes 2000a, b; Schmidt et al. 2002). Specifically, velocities of forward and transverse displacement are predicted to vary sinusoidally during locomotion, with peak forward velocity occurring in phase with peak rightward and leftward transverse velocities. When transverse velocity of the center of mass is assigned negative values whenever the center of mass deviates to the left of the net axis of travel and positive values when to the right (as in Fig. 3), the wavelength of transverse velocity should be twice that of forward velocity. Kinematic analysis of the cockroach *Blaberus discoidalis* largely corroborates predictions of the model (Schmidt et al. 2002).

Kinematics in running *Leiobunum* was also roughly consistent with the LLS model (Fig. 3). Specifically, the transverse-velocity sinusoid has a wavelength about twice that of the forward velocity and the peaks and troughs of the transverse velocity plot occur near the peaks in forward velocity. However, in contrast to the fairly simple sinusoid displayed by forward velocity, transverse velocity showed a more complex pattern and may even have had a low-amplitude, short-wavelength velocity fluctuation superimposed on the predicted waveform. In addition, peaks in the transverse waveform appeared to precede peaks in forward velocity rather than occurring simultaneously as predicted. Significantly, the phase difference between the forward and transverse velocity peaks was also observed in the cockroach (Schmidt et al. 2002: fig. 6). The overall similarity of the predictions of the LLS model and empirical observations indicate that lateral springs are probably important for locomotion and specifically for stabilization. However, given that two arthropods deviate from expectations in the same manner, the LLS model probably needs refinement.

Locations of possible leg springs.—Compatibility of locomotor kinematics with the SLIP and LLS models indicate that elastic energy storage is a significant component of locomotion in *L. vittatum*, but the anatomical placement of appropriate elastic mechanisms is not known. The existence of highly efficient springs has already been documented at the tibia-tarsus joint in *L. vittatum*, although its precise role in locomotion has yet to be determined (Sensenig & Shultz 2003). The tibia-tarsus joint of each leg is spanned by a pair of deformable sclerites that store energy during flexion and return up to 90% of this energy during extension. Gravity can potentially assist muscles in deforming the elastic sclerites of legs 1 and 3 during locomotion, but flexion of this joint in leg 4 occurs only when the leg is off the ground and it is unlikely that the sclerites could be loaded by gravity.

In principle, any muscle-tendon complex can store externally generated mechanical energy if its contractile and/or connective elements have intrinsic tensile resilience and experience externally generated tensile forces

(McMahon 1990). Shultz (2000) identified 13 intrinsic leg muscles in *Leiobunum*, but the muscle-tendon complex of the claw (Fig. 1) seems particularly well suited to act as a spring. Here a long tendon attaches to the claw distally, spans the length of the multisegmented tarsus, and attaches proximally in the tibia and patella via muscles (Guffey et al. 2000; Shultz 2000). The tarsus is typically curved when supporting the animal, both when standing and during locomotion (Fig. 2). Forces from gravity, propulsive movements or transverse perturbations during locomotion may bend the tarsus further, thereby increasing tension on the muscle-tendon complex and storing energy within its elastic elements. Elastic energy might then be converted to kinetic energy toward the opposite direction once the tensile load was released causing the tendon to shorten and the tarsus to "unbend." A comparable mechanism exists in other arthropods, where elasticity of the tarsal tendon maintains postural equilibrium in the face of external perturbation (Frazier et al. 1999). However, determining the precise role of the claw tendon and other potentially elastic elements in *Leiobunum* will require additional investigation.

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2006 (2007). The Journal of Arachnology 34:634–635

SHORT COMMUNICATION

THE IDENTITY OF *CENTRUROIDES ELEGANS EDENTULUS* (SCORPIONES, BUTHIDAE)

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ABSTRACT. A lectotype is designated for *Centruroides elegans edentulus* Werner 1939, originally described from Cuernavaca, Morelos, Mexico. It is declared a junior synonym of *Centruroides limpidus* (Karsch 1879).

Keywords: Cuernavaca, Morelos, Mexico, lectotype, *limpidus*

The scorpion *Centruroides elegans edentulus* Werner 1939 was originally described on the basis of three "paratypen" collected in Cuernavaca, Estado de Morelos, México (Werner 1939), and has remained neglected and ignored ever since. It is not mentioned by Stahnke & Calos (1977) in their key to the species in the genus, or by Beutelspacher (2000) in a catalog of the scorpions of México. A recent thorough survey of the scorpions of Morelos by the senior author (Córdova-Athanasiadis 2005) failed to reveal the presence of the species in that state, prompting us to examine the types and ascertain the taxonomic status of the subspecies.

The original description of *C. elegans edentulus* is very brief (only six lines long) and not very informative: from the name chosen by Werner we guessed that the taxon lacks a subaculear spine or tooth ("edentulus" means toothless), a very variable character in the genus *Centruroides* Marx 1890; and since it was compared to *Centruroides pallidiceps* Pocock 1902, we expected a "non-striped" or uniformly pale colored taxon.

Centruroides elegans (Thorell 1876) occurs on the western slopes of the Sierra Madre Occidental, from Oaxaca north to Nayarit and southern Sinaloa (Beutelspacher 2000; Fet et al. 2000): it is a "striped" species recognized by having dark coloration (spots) submedially on the pre-tergites and unmarked post-tergites, and generally has a well-developed subaculear spine. *Centruroides limpidus limpidus* (Karsch 1879) is found in the Balsas River basin, between the eastern slopes of the Sierra Madre Occidental and south of the Sierra Madre Transversal (Beutelspacher 2000; Fet et al. 2000): it is also a "striped" species with intense submedian dark spots covering both the pre- and post-tergites, and its subaculear spine is usually vestigial (Hoffmann 1932).

The three paratypes of *C. elegans edentulus* are deposited at the Zoologisches Institut und Museum, Hamburg Universität, Germany, and we recently examined them while they were on loan to the American Museum of Natural History, New York. One specimen, although immersed in alcohol, had been previously dried so it is totally discolored, and is missing the entire metasoma and is therefore taxonomically worthless. A second specimen is an adult male in good condition and is hereby designated the lectotype of the subspecies: the carapace is 5.6 mm long and has four fuscous longitudinal stripes–the submedians are somewhat faded with time, and the laterals are irregular and underlie large granules; the color on the tergites is also faded, with very diffuse markings on the anterior margins and faint markings medially and posteriorly; the pectinal tooth count is 25–26; the subaculear spine is vestigial, represented by a very small granule. The third specimen is an adult female hereby designated a paralectotype: the carapace is 5.9 mm long and has four distinct longitudinal fuscous lines (more clearly defined than on the lectotype); tergites I–IV have anterior and posterior spots well defined, and on V–VII the anterior spot is well defined and the posterior spot is diffuse but clearly present; the basal pectinal plate has a small central indentation, and the pectinal tooth count is 23–24; the subaculear spine is vestigial to obsolete, its presence indicated by a small bump.

We could find no differences between the lectotype and paralectotype of *C. elegans edentulus* and samples of *C. limpidus limpidus* from Cuernavaca and other nearby localities in Morelos; therefore, we propose that the former is a junior synonym of the latter. We have examined 1189 specimens of the genus *Centruroides* from 82 localities in Morelos, and aside from an introduced population of *Centruroides margaritatus* (Gervais 1841) in the city of Cuernavaca, they all represent either *C. limpidus limpidus* or *C. balsasensis* Ponce & Francke. In our opinion, published records of *C. elegans* from Morelos (Beutelspacher 2000) are based on misidentifications of *C. limpidus*.

We are thankful to the Facultad de Ciencias Biologicas, Universidad Autonoma del Estado de Morelos and Laboratorios Silanes for supporting our field work; to Dr Hieronymus Dastych of Hamburg for the loan of the types of *C. elegans edentulus*; to Dr Lorenzo Prendini of New York for arranging that loan and hosting our visit; and to Mr Edmundo Gonzalez-Santillán for his assistance on the project.

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SHORT COMMUNICATION

THE MALE OF *SUFFASIA ATTIDIYA* (ARANEAE, ZODARIIDAE)

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ABSTRACT. *Suffasia attidiya* was previously known only from females. This paper describes males collected from the type locality. Males of *S. attidiya* can be recognized by the following combination of characters: tibia with stout retrolateral apophysis; triangular dorsal cymbial extension; cymbial flange attached at its center to the cymbium; embolus with a base positioned under the proximal part of tegulum; long tapering, outwards pointing tegular apophysis.

Keywords: taxonomy, Sri Lanka, Oriental region

The genus *Suffasia* combines autapomorphies of the subfamilies Zodariinae and Storeninae (Jocqué 1992; Dankittipakul & Jocqué 2004) and is therefore a key zodariid genus. It is known only from the Indo-Oriental region; of the four described species two are from Sri Lanka (Platnick 2005). In the original description of the two species from Sri Lanka by Benjamin and Jocqué (2000), one of them, *S. attidiya*, was described only from females. During recent collecting at the type locality, I was able to collect two males which are described below.

Preparation of material and drawings were done as in Benjamin (2004), and the description follows the format used by Benjamin and Jocqué (2000). Specimens examined are deposited in the Muséum d'histoire naturelle, Genève (MHNG) and the Naturhistorisches Museum, Basel (NMB).

TAXONOMY

Family Zodariidae Thorell 1881

Genus *Suffasia* Jocqué 1991

Suffasia Jocqué 1991: 146.

Type species.—*Suffucia tigrina* Simon 1893 by original designation.

Remarks.—The genus *Suffasia* contains four species (Jocqué 1991, 1992; Benjamin & Jocqué 2000) and is currently known only from India, Nepal and Sri Lanka (Platnick 2005).

Suffasia attidiya Benjamin & Jocqué 2000 (Figs. 1–3)

Suffasia attidiya Benjamin & Jocqué 2000: 102, figs. 8–12.

Material examined.—SRI LANKA: *Western Province*: 2 ♂, Colombo, Bellanwila-Attidiya (approximately 6°50′N, 79°54′E), mean elevation 0.6 m asl, 22 February 2000, S.P. Benjamin (1 ♂ MHNG, 1 ♂ NMB).

Diagnosis.—The male of *S. attidiya* can be recognized by the following combination of characters. The tibia with stout retrolateral apophysis (RTA), a triangular dorsal cymbial extension (DE), cymbial flange (CF) attached at its center to the cymbium. Embolus with a base positioned under the proximal part of tegulum (EB) and the long tapering, outwards pointing tegular apophysis (TA). The second species known from Sri Lanka, *S. mahasumana* Benjamin & Jocqué 2000, possesses a tibia with a longer retrolateral aphophysis, oval dorsal cymbial extension, cymbial flange attached at its base to the cymbium. Embolus with an outward projecting base visible in the dorsal view and a shorter broad-based, out and forwards pointing, tegular apophysis. Benjamin and Jocqué (2000) presented a diagnosis for the females.

Description.—*Male:* Mostly as described for female. Coloration and markings as in female (see Benjamin and Jocqué 2000: figs. 11, 12). Palp (Figs. 1–3): Tibia with stout retrolateral apophysis. Cymbium with a well-developed triangular dorsal cymbial extension (DE), dorsolateral cymbial flange attached at its center to the cymbium (CF), extending lateral cymbial concavity carrying some sensorial hairs in superior part. Embolus long, origi-

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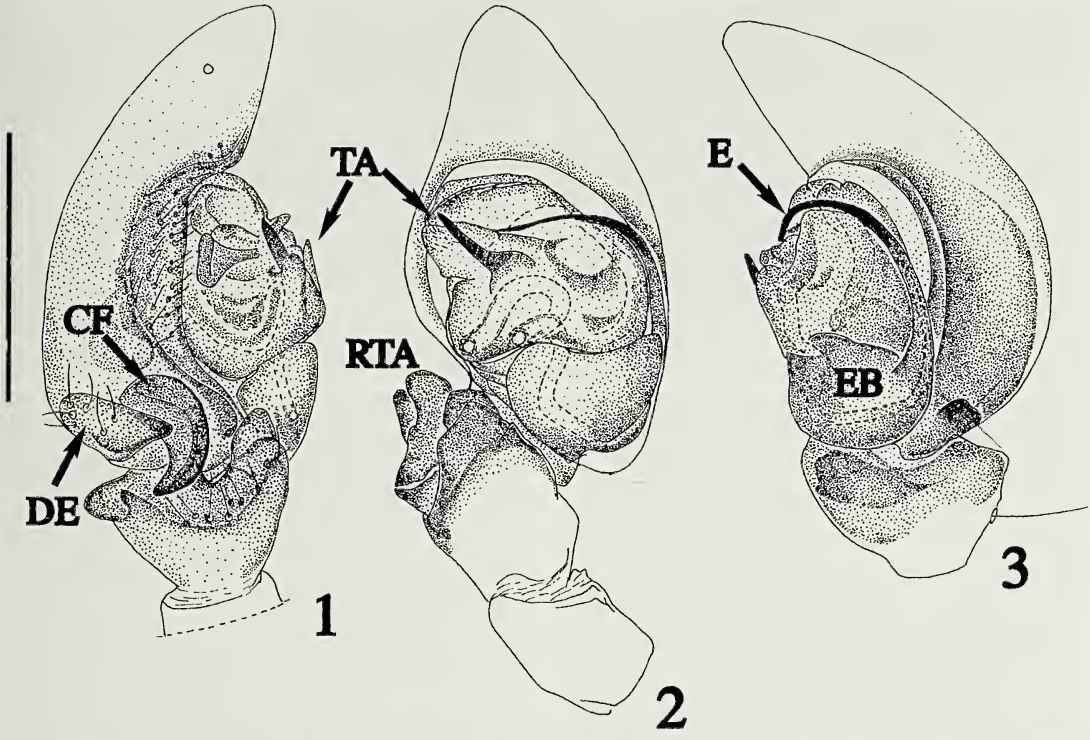

Figures 1–3.—*Suffasia attidiya* Benjamin & Jocqué, male from Bellanwila-Attidiya: 1. Male palp, retrolateral view; 2. Male palp, ventral view; 3. Male palp, prolateral view. CF = cymbial flange; DE = dorsal cymbial extension; E = embolus; EB = base of embolus; RTA = retrolateral tibial aphophysis; TA = tegular apophysis. Scale line = 0.2 mm.

nating from proximal part of tegulum, base hidden. Tegular apophysis, long, tapering, pointing outwards (TA).

Measurements (mm): Total length 2.2; prosoma length 1.1; prosoma width 0.7. Leg 1: femur 0.6; patella 0.2; tibia 0.4; metatarsus 0.6; tarsus 0.4.

Female: see Benjamin and Jocqué (2000).

Distribution.—*Suffasia attidiya* is known only from two localities: Bellanwila-Attidiya sanctuary and Kalugala, Labugama Forest Reserve in the Western Province of Sri Lanka.

I thank Mr. A. H. Sumanasena (Department of Wild Life Conservation, Colombo) for providing a research permit. Dr. Peter Schwendinger (MHNG) is thanked for assistance, hospitality, discussion and enabling the study of comparative material under his care. I am grateful to Barbara Baehr and an anonymous reviewer for helpful comments.

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SHORT COMMUNICATION

NOTES ON WEB AND WEB PLASTICITY AND DESCRIPTION OF THE MALE OF *ACHAEARANEA HIEROGLYPHICA* (MELLO-LEITÃO) (ARANEAE, THERIDIIDAE)

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ABSTRACT. Cobweb spiders (Theridiidae) exhibit a rich variety of web designs. Current knowledge of theridiid web architecture and evolution indicates that theridiid web design shows high within-taxon diversity and frequent convergence. Here we redescribe *Achaearanea hieroglyphica* (Mello-Leitão 1940), including the first description of the male, and document in this species (1) an unusual web design and (2) two dramatically different type of webs.

Keywords: Orbicularia, spider webs, taxonomy, web evolution

We made observations on *A. hieroglyphica* at the Les Nouragues Field Station, on the "Montagnes Balenfois" massif, Commune Règina, French Guiana, 4°04′08.64″N, 52°40′08.20″W, on 13–25 November 2005. The field station is placed in a 85 km^2 tract of undisturbed lowland blackwater rainforest at ~50 m elevation.

We documented two types of *A. hieroglyphica* webs made by the two mature females we found (Figs. 1–4). In web one (Figs. 1–3) the spider rested against the underside of a live leaf, within a simple tangle retreat. From that leaf, two non-sticky, planar sheets, situated at opposite edges of the leaf, were extended at an angle (not close to either vertical or horizontal orientation) to nearby leaves. A dense cluster of gumfoot lines—lines with sticky silk restricted to their distal tips—extended from the retreat to a leaf directly below it. In other known theridiids, planar sheets are relatively rare and very few are known that slant in this way, while gumfoot lines are common. Webs with both are known from only some *Latrodectus* species and an undescribed species close to *Chrysso cambridgei* (Petrunkevitch 1911), although in these, the sheets do not slant. In web two (Fig. 4), the spider rested against the underside of a dead leaf that was suspended in the web. This web was a typical theridiid tangle web, with gumfoot lines to the substrate below, and lacked any sheets.

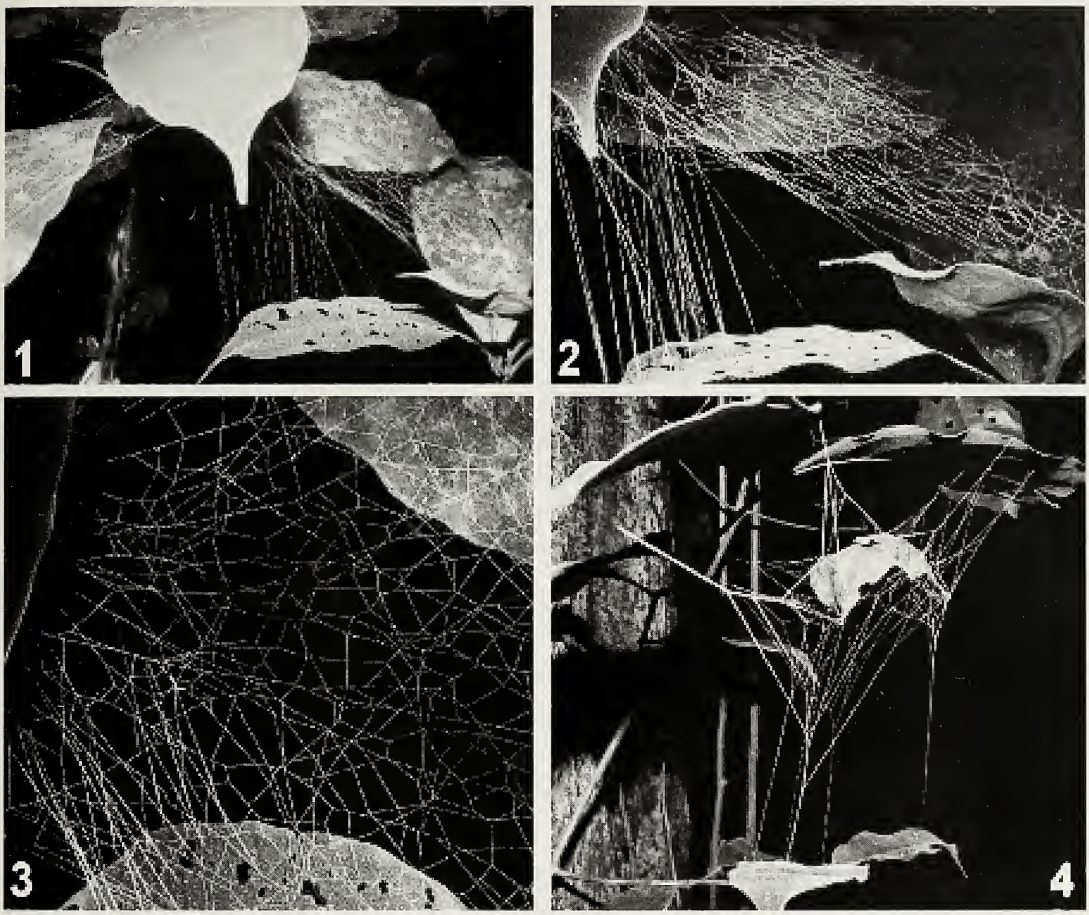
Our observations extend the amazing diversity, and within-species plasticity, of web design in Theridiidae. Considering that only two webs were seen, the use of different structures to make a retreat, the presence of planar sheets in one web but not the other, and the different arrangements of the gumfoot lines demonstrate striking plasticity. Webs remain unknown for the vast majority of theridiid species, and almost all current knowledge is based on photographs of single webs (Eberhard et al. submitted). To understand the degree of within-species web plasticity, future comparative studies of theridiid webs would do well to explore both webs of multiple individuals, and multiple webs made by the same individual.

Specimens are housed in the following institutions: National Museum of Natural History, Smithsonian Institution, Washington DC (NMNH); National Museum, Rio de Janeiro (NMRJ); Muséum National d'Histoire Naturelle, Paris (MNHN). All measurements are in mm.

TAXONOMY

Family Theridiidae Sundevall 1833
Genus *Achaearanea* Strand 1929
Achaearanea hieroglyphica
(Mello-Leitão 1940)
Figs. 1–11

Achaea hieroglyphica Mello-Leitão 1940:202.
Chrysso pentagona Caporiacco 1954:75, figs. 12–12a.



Figures 1–4.—*Achaearanea hieroglyphica* webs. 1. Web one; the combination of a slanting planar sheet and typical gumfoot lines is very unusual among theridiids. Spider rests underneath the protruding leaf. 2. Closer view of one of the planar sheets and the gumfoot lines. 3. Details of planar sheet. 4. Web two, having only a few gumfoot lines and lacking a planar sheet, with the spider resting under a dead leaf suspended in the webbing.

Achaearanea pentagona (Caporiacco): Levi & Levi 1962:211; Levi 1963:202, figs. 1–3.

Achaearanea hieroglyphica (Mello-Leitão): Levi 1967:22.

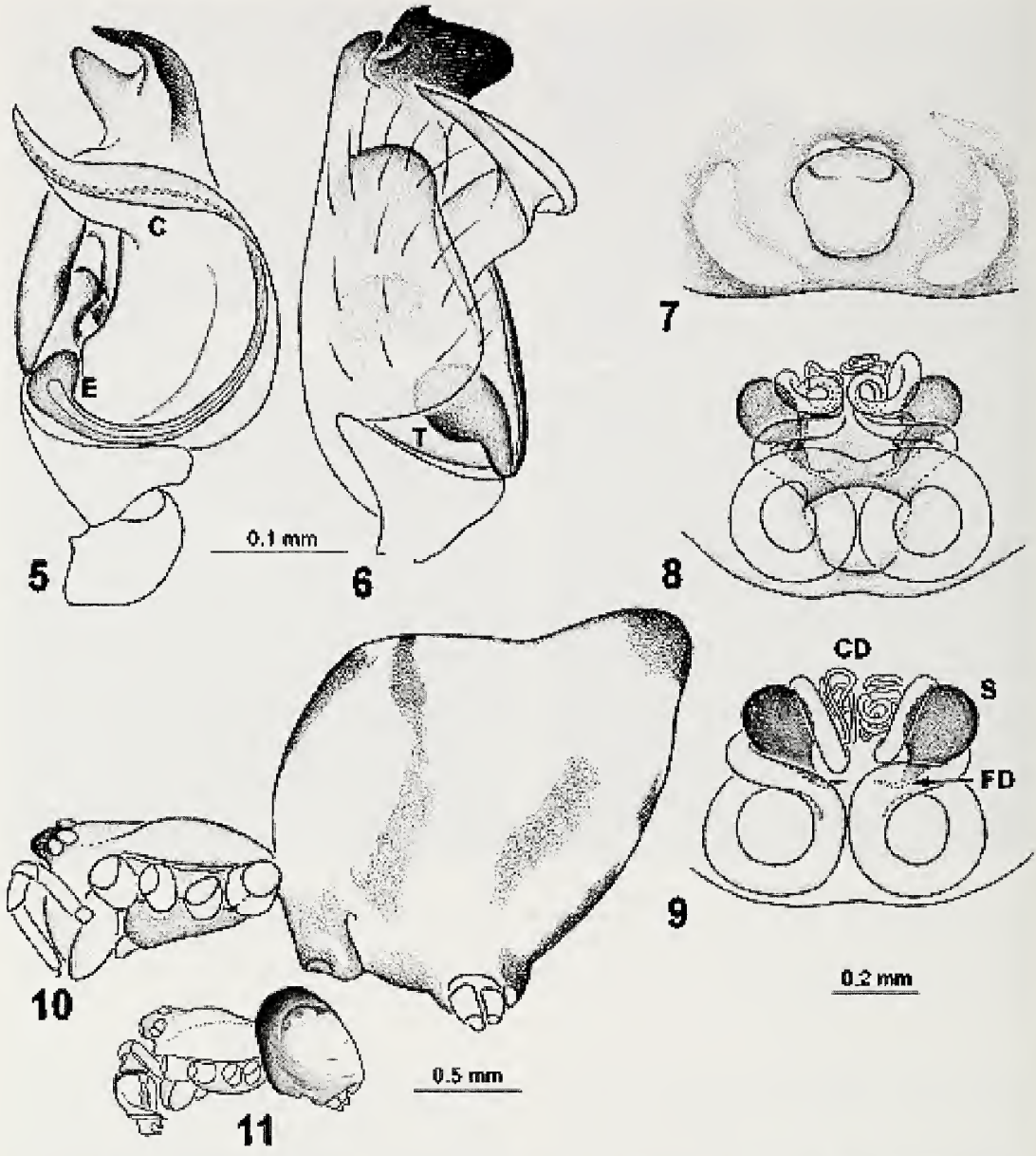
Type specimens.—*Achaea hieroglyphica:* holotype female, BRAZIL, *Espírito Santo*, Colatina [19°32′S, 40°37′W] (NMRJ) (see Levi 1967), not examined.

Chrysso pentagona: holotype female, FRENCH GUIANA, Goudronville [5°01′N, 52°39′W] (MNHN) (see Levi 1967), not examined.

Material examined.—FRENCH GUIANA: Commune Règina, Les Nouragues Field Station, 4°04′08.64″N, 52°40′08.20″W, 13–25 November 2005, J. Coddington, N. Scharff, J. Miller, I. Agnarsson, M. Kuntner, D. DeRoche (NMNH).

Diagnosis.—Males of *Achaearanea hieroglyphica* differ from most *Achaearanea* species by the strongly modified cymbium with two distal, pointed, apophyses (Figs. 5–6). It is similar to the type species *A. trapezoidalis* (Taczanowski 1873), but differs from it in having a much shorter embolus (Figs. 5–6). Females differ from most other *Achaearanea* by the extremely long and complex trajectory of the copulatory duct, and from *A. trapezoidalis* by the less regular, and asymmetric, pathways of the copulatory ducts (Fig. 9).

Description.—*Male:* (Les Nouragues Field Station). Total length 1.25. Prosoma 0.60 long, 0.55 wide, brown, cephalic area slightly darker. Sternum 0.40 long, 0.35 wide, reddish-brown. Abdomen 0.60 long, 0.80 wide, higher than long, proximal half dark grey, distal half white, pattern as in Fig. 11. Colulus and colular setae absent. Eyes subequal in size about 0.08 diameter. Clypeus height about 2.0 times one AME diameter. Leg I femur 0.90, patella 0.15, tibia 0.70, metatarsus 0.60, tarsus 0.25.



Figures 5–11.—*Achaearanea hieroglyphica*: 5. Male palp, ventral view. 6. Male palp, mesal view. 7. Epigynum, ventral view. 8. Epigynum, cleared in KOH, ventral view. 9. Epigynum, cleared, dorsal view. 10. Female habitus, ectal view. 11. Male habitus, ectal view. Male and female are drawn to scale; such sexual size dimorphism is not uncommon in *Achaearanea* and relatives. C = conductor, CD = copulatory ducts, E = embolus, FD = fertilization ducts, S = spermathecae, T = tegulum.

Chelicerae with a single promarginal tooth, none retrolaterally. Legs pale orange with portions of femur and tibia I darker, and narrow dark annulations at distal tip of most segments. Legs IV darker than other legs. Abdominal stridulatory picks, and epiandrous gland spigots not visible with light microscopy.

Palpal organ with large sinuous conductor, embolus spiraling counter-clockwise in left palp, distal part inside groove in conductor, theridiid tegular apophysis and median apophysis apparently absent. Cymbium with diagnostic paired apophysis distally, the ectal one distinctly ridged (Figs. 5–6).

Female: (Les Nouragues Field Station): Total length 4.10. Prosoma 1.50 long, 1.35 wide, light brown with darker rim, and center orange. Sternum

0.90 long, 0.65 wide, dark grey. Abdomen 2.90 long, 1.85 wide, light gray with several dark and some white stripes, pattern as in Fig. 10. Colulus and colular setae absent. Eyes subequal in size about 0.10 diameter. Clypeus height about 2.7 times one AME diameter. Leg I femur 2.90, patella 0.60, tibia 2.00, metatarsus 2.20, tarsus 0.90. Legs pale yellowish with patella and distal parts of femora and tibia darker brown. Palpal claw semi-palmate (see Agnarsson 2004). Chelicera with one promarginal tooth, none retrolaterally.

Epigynum with a single central depression, apically leading to the paired copulatory openings. Copulatory ducts very long, basal section forms a near-circular loop, but the trajectory becomes increasingly irregular and asymmetric distally (Figs. 7–9).

Variation.—Female total length 4.10–5.00, first femur 2.90–3.55. Male total length 1.10–1.25, first femur 0.80–0.90.

Distribution.—French Guiana, Brazil, Peru.

Matching sexes.—Given that the male and female were not collected from the same webs, and they differ considerably in both size and color pattern it remains possible that they are not conspecific. However, substantial dimorphisms in sexual size and color pattern, are known in some *Achaearanea* (e.g., Levi 1963). The primary evidence for matching of the sexes is their mutual resemblance to the morphologically unusual *A. trapezoidalis* (see e.g., Levi & Levi 1962), the type species of the genus. The male palpal cymbium has unusual paired distal apophyses, although similar ones are present in *A. trapezoidalis*. The epigynum resembles that of *A. trapezoidalis*, with extremely long copulatory ducts that narrow gradually along most of their length, and twist profusely.

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SHORT COMMUNICATION

SUBSOCIALITY IN *HELVIBIS THORELLI* KEYSERLING 1884 (ARANEAE, THERIDIIDAE, THERIDIINAE) FROM FRENCH GUIANA

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ABSTRACT. Preliminary observations on *Helvibis thorelli* (Theridiidae) in French Guiana suggest a typical subsocial behavior in this species, with nests consisting of a mother and her offspring who collaborate in prey capture. Communal feeding occurs over several juvenile instars. Subsociality has previously been described in three theridiid genera (*Achaearanea*, *Anelosimus*, *Theridion*) and predicted to occur in further genera of the subfamily Theridiinae. Our findings support this prediction and have important implications for comparative studies as they add another independent observation of social behavior: current phylogenetic knowledge implies subsociality evolved independently in each of these genera.

Keywords: evolution of sociality, maternal care, communal feeding

Subsociality is rare but phylogenetically scattered in spiders with about 30–40 species distributed in Amaurobiidae, Eresidae, Lycosidae, Pisauridae, Salticidae, Scytodidae, Thomisidae, and Theridiidae (Avilés 1997; Agnarsson et al. 2006). Subsocial spiders form ephemeral colonies consisting of a single mother and offspring; these colonies typically persist until the spiderlings disperse close to adulthood (Schneider 2002; Powers & Avilés 2003), although the exact timing of dispersal may depend on food availability (Schneider 1995; Kim 2000). Subsociality entails not only extended maternal care and mutual tolerance (e.g., Salomon et al. 2005 and references therein) but also cooperation between individuals within a colony, where juveniles actively partake in the colony functions (Agnarsson et al. 2006), for example in prey capture (Kim et al. 2005). Three theridiid genera, *Achaearanea*, *Anelosimus*, and *Theridion*, are known to contain subsocial species and current phylogenetic evidence suggests subsociality evolved independently in each genus (Agnarsson 2002, 2004, 2005, 2006; Avilés et al. 2006; Agnarsson et al. 2006). The phylogenetic distribution of subsociality is important in understanding the evolutionary history of social behavior. Social spiders form permanent colonies that contain anywhere from a few to over 10,000 individuals. In these colonies siblings will mate with each other and dispersal is rare (Avilés 1997). As far as known, social species occur only within subsocial lineages, although detailed phylogenetic evidence supporting this is, thus far, only available in Theridiidae (Agnarsson 2004, 2005, 2006). All available evidence, therefore, suggests that social spiders evolved from subsocial ancestors (e.g., Avilés 1997; Schneider 2002; Agnarsson 2004, 2006; Bilde et al. 2005; Agnarsson & Zhang 2006; Agnarsson et al. 2006). Subsociality, in turn, has only evolved in lineages where maternal care beyond care of the egg sac is common (Avilés 1997; Agnarsson 2002, 2004; Schneider 2002). The link between maternal care and subsociality led to a prediction: because maternal care in theridiids optimized to the "lost colulus clade" (*Anelosimus* plus Theridiinae, see Agnarsson 2004 fig. 102), additional discoveries of subsocial species could be predicted within that node (Agnarsson 2004; Agnarsson & Kuntner 2005; Miller & Agnarsson 2005). Here we corroborate this prediction and report the discovery of subsociality in a fourth genus in the lost colulus clade, *Helvibis*.

We made observations on subsocial *Helvibis thorelli* Keyserling 1884 colonies (Figs. 1–6) on three

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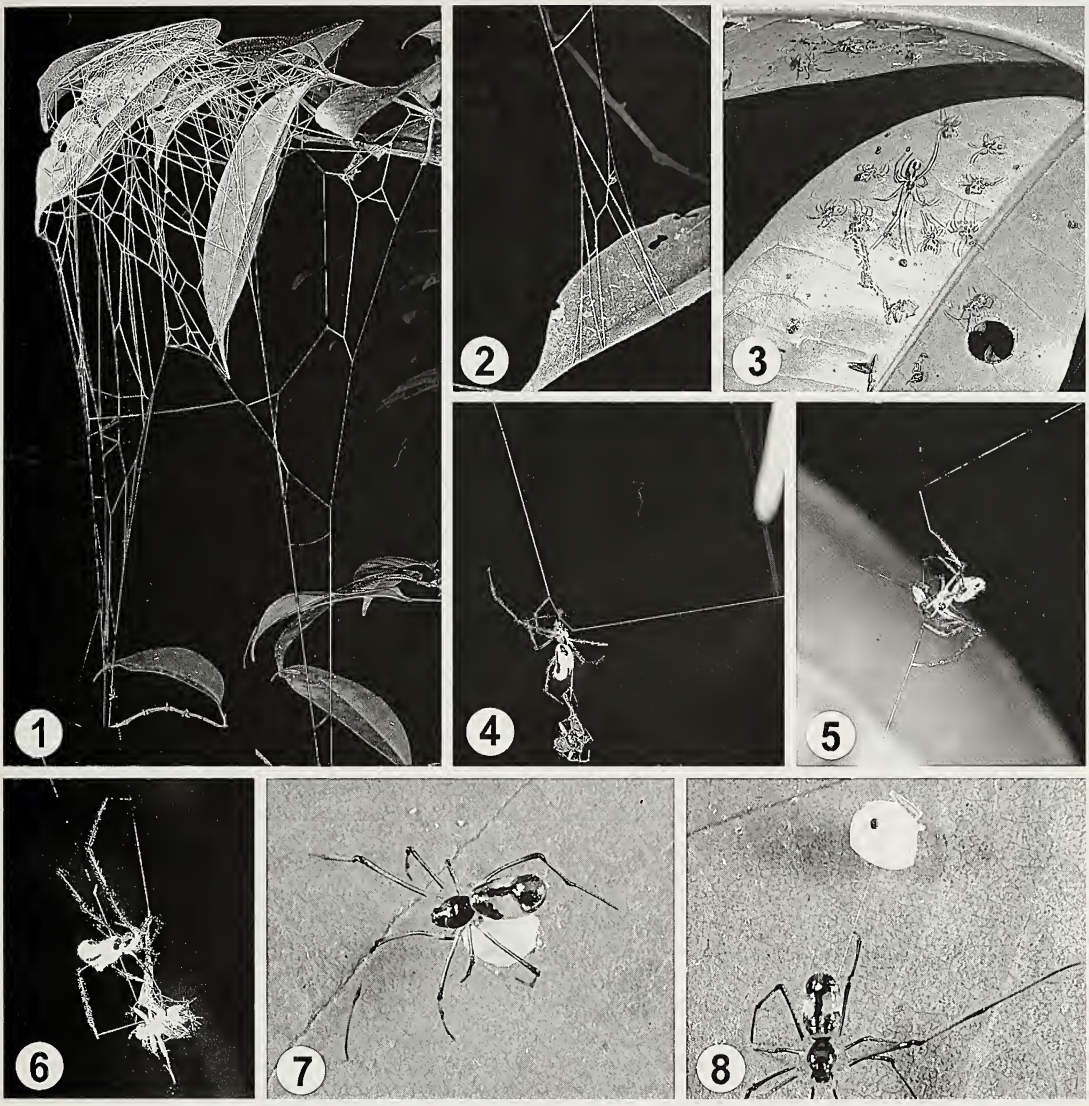

Figures 1–8.—*Helvibis thorelli*. 1. Subsocial web, ~80 cm tall. 2. Attachments of web. 3. Adult female and nine 4th or 5th instar juveniles resting under leaf. 4. Female transporting prey to retreat, attached to the spinnerets and held with one leg IV. 5. Subadult male catching a phlobotomine fly. 6. Female wrap-attacking a cricket. 7. Female with egg sac; photo by M. Kuntner. 8. Female pulling eggsac with a line attached to the spinnerets and held with one leg IV, the same way a prey is carried back to the retreat; photo by M. Kuntner.

consecutive nights (18–20 September 2005) at the Les Nouragues Field Station, on the "Montagnes Balenfois" massif, Commune Règina, French Guiana (4°04′08.64″N, 52°40′08.20″W). The field station is placed in an 85 km² tract of undisturbed lowland blackwater rainforest at approximately 50 m elevation. Vouchers from this study are deposited in the National Museum of Natural History, Smithsonian Institution.

We saw dozens of *H. thorelli* (Figs. 1–8) webs in this forest. The spiders rested against the underside of live leaves. The webs typically consisted of a network of lines densely-spaced near the resting site with longer and sparser lines further away, which attached the web to other leaves and, in some cases, to the ground (Figs. 1, 2). All the long lines, and some of the short lines, are sticky along almost their entire length, but the ends of the long line segments are non-sticky, unlike typical "gumfoot" webs of some theridiids (e.g., Agnarsson & Coddington 2006) but identical to the web of the social *Theridion nigroannulatum* Keyserling 1884 (Avilés

et al. 2006). Nearly all the webs we saw contained a single female, about a third of them guarding an egg sac (Figs. 7, 8; egg sacs contained on average 20 eggs, range 14–24, $n = 5$), while three webs contained the mother and her offspring. Two webs contained a mother and small, probably first or second instar, juveniles and one contained the mother and 13 large juveniles, which, based on the presence of two subadult males, we estimated as 4th or 5th instars (Figs. 1–6). The latter subsocial web was constructed under two adjacent leaves (Fig. 1). The spiders rested in close proximity to each other (Fig. 3). Animals interacted frequently, mostly by touching the first pair of legs without aggression.

We observed prey capture and feeding, under dimmed white light, on naturally caught and introduced prey in two of the subsocial webs. First, in the web containing large juveniles, a phlebotomine fly impacted one of the long sticky lines. After a few minutes, spiders noticeably reacted to the vibrations caused by its struggling. A juvenile responded first by descending on a sticky line adjacent to the line adhering to the prey. Shortly thereafter, the mother descended on the line containing the prey and began a typical sticky silk wrap attack (e.g., Griswold et al. 1998) on the fly before biting. Both spiders walked slowly but apparently without difficulty on the gluey silk line but spun another non-sticky line while walking. The mother wrapped and left the prey at the impact site, and both juvenile and mother ascended rapidly to the leaf retreat on their newly spun non-sticky lines. A few minutes later, the mother descended again in a fast descent down the non-sticky line, cut the prey loose, and carried it on a line attached to the spinnerets and held with one leg IV to the edge of the retreat where she continued to wrap it. Two juveniles approached the mother and prey, but she broke away from them and resumed wrapping. Approach of juveniles and maternal turning away was repeated several times until the mother left the prey and two juveniles began feeding on it together. Later, two additional juveniles began to feed as well. No aggression was seen between the individuals during this behavioral sequence.

We then entangled a small (< 1 cm) cricket on two long sticky lines. Several minutes later the mother reacted to the vibrations by descending and subduing the prey as previously described. A juvenile then arrived at the prey site and appeared to bite and wrap the prey simultaneously with the mother. The animals again left the prey at the attack location, and returned towards the retreat. Before reaching the retreat, the mother returned and started cutting the prey free from the web, thereby destroying several of the long sticky lines. She returned to the retreat with the prey attached as before and eventually juveniles began to feed on the prey. A second phlebotomine fly impacted the web, was detected, attacked, carried to the retreat, and eaten by a subadult male using the same behaviors as the mother (Fig. 5). Finally, a beetle impacted the web and after at least a five minute delay, the mother approached, touched it repeatedly with her first legs but did not wrap it. She returned to the retreat and the beetle eventually broke loose. We also observed prey catching in one of the subsocial webs with small juveniles, where prey handling was identical, except that the small juveniles did not react in any way to prey getting stuck in the web or to the mother attacking but stayed in the retreat.

Even though only a few colonies were seen, *H. thorelli* clearly behaves like a typical subsocial theridiid spider: a nest is founded by a solitary female, a colony consists of a mother and her offspring that disperse near adulthood, colony members exhibit non-aggressive interactions, communal prey attack and feeding is demonstrated, and the mother catches prey that is then left for the juveniles to feed on. This constitutes the known fourth independent origin of subsocial behavior in theridiids, one each in *Anelosimus*, *Achaearanea*, *Theridion*, and *Helvibis*. Both molecular (Arnedo et al. 2004) and morphological (Agnarsson 2004; Agnarsson et al. 2006) data place *Helvibis* in Theridiinae, although morphology places it as sister to *Theridion* and molecules as sister to *Chrysso*. Both placements require the novel origin of subsociality in *Helvibis* as the two genera are primitively solitary.

The discovery of subsociality in *Helvibis* corroborates predictions derived from the phylogenetic distribution of maternal care (Agnarsson 2002, 2004; Agnarsson & Kuntner 2005), and provides another evolutionary replicate for comparative studies of subsocial behavior and the evolution of sociality. Recently, co-workers have discovered additional social and/or subsocial species: e.g., *Anelosimus oritoyacu* Agnarsson 2006, *A. guacamayos* Agnarsson 2006, *A. puravida* Agnarsson 2006, *A. dubiosus* (Keyserling 1891), and *Theridion nigroannulatum* Keyserling 1884 (Marques et al. 1998; Agnarsson 2006; Avilés et al. 2006). Probably many more subsocial and social spider species await discovery. More fieldwork is an urgent priority.

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SHORT COMMUNICATION

ON THE VENEZUELAN SPECIES OF JUMPING SPIDER DESCRIBED BY SCHENKEL (ARANEAE, SALTICIDAE)

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ABSTRACT. Two new synonyms are established in Salticidae: *Menemerus falconensis* Schenkel 1953 is designated as a junior synonym of *Freya infuscata* (F.O. Pickard-Cambridge 1901); and *Phiale albovittata* Schenkel 1953 is designated as a junior synonym of *Freya perelegans* Simon 1902. In addition, the new combination *Cotinusa furcifera* (Schenkel 1953) is proposed for *Breda furcifera* Schenkel 1953.

Keywords: South America, taxonomy, *Cotinusa*, *Freya*

After the examination of some arachnids brought from Venezuela by Dr. K. Wiedenmeyer, Schenkel (1953) published a paper describing several species, including six species of jumping spiders. The original descriptions, however, are poor and the drawings presented do not allow their identification.

Although Dr. M.E. Galiano had already examined the type specimens of these salticids, only three nominal species were redescribed and well illustrated during her revisions. *Lyssomanes minor* Schenkel 1953 was redescribed by Galiano (1962); *Menemerus acostae* Schenkel 1953 and *Lyssomanes wiedenmeyeri* Schenkel 1953 were treated as junior synonyms of *Pachomius dybowskii* (Taczanowski 1871) and *Lyssomanes elegans* F.O. Pickard-Cambridge 1900, respectively, by Galiano (1963a, 1980). The other three species remained unrecognizable until now.

Recently, Dr. Ambros Hänggi kindly sent us the type material of the species not recorded by Galiano, namely *Breda furcifera* Schenkel 1953, *Menemerus falconensis* Schenkel 1953 and *Phiale albovittata* Schenkel 1953. In this paper we present two new synonymies and a new combination for these nominal species as well as redescriptions and illustrations where necessary.

The material examined is deposited in the Naturhistorisches Museum Basel, Basel, Switzerland (NMB, A. Hänggi). The measurements are in millimeters. The following abbreviations were used: RTA = retrolateral tibial apophysis; AME = anterior median eyes; PME = posterior median eyes; PLE = posterior lateral eyes; d = dorsal; p = prolateral; r = retrolateral; v = ventral; di = distal.

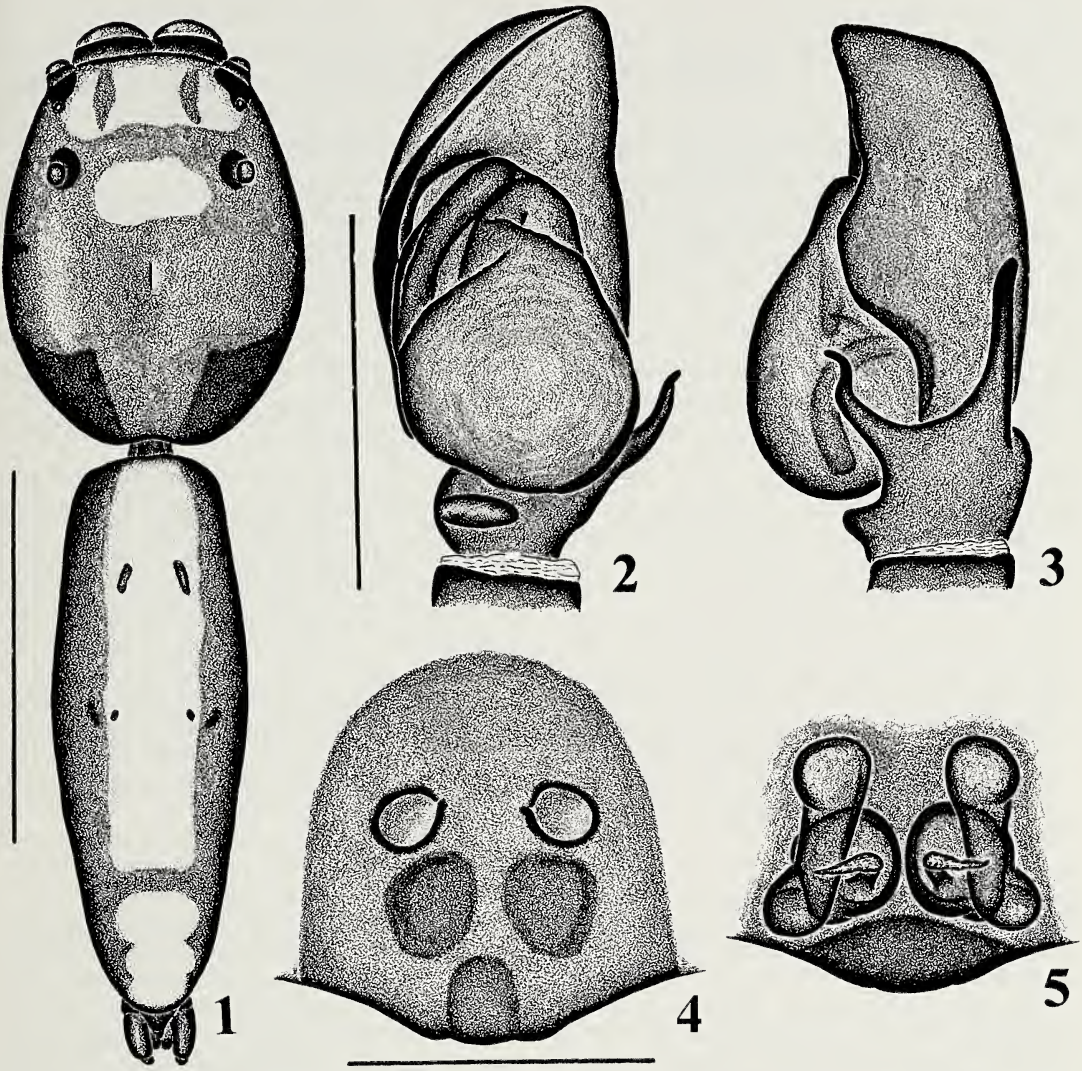
TAXONOMY

Family Salticidae Blackwall 1841
Genus *Cotinusa* Simon 1900
Cotinusa furcifera (Schenkel 1953)
NEW COMBINATION
Figs. 1–3

Breda furcifera Schenkel 1953:53, figs. 46a–b; Platnick 2006.

Material examined.—VENEZUELA: *Falcón*: male holotype, El Pozón, Distrito Acosta (12°06′N, 70°00′W), October 1924–January 1925, K. Widenmeyer (NMB 2256).

Description.—Total length: 5.40. Carapace light brown, dark laterally, 2.25 long, 1.60 wide, 0.90 high (Fig. 1). Ocular quadrangle 0.85 long, black rings around eyes, light areas between the PLE and among the PME and the anterior eyes (Fig. 1); internal dark structures of the AME seen through the translucent tegument. Anterior eye row 1.07 wide, posterior 1.10 wide. Chelicerae with one tooth with four tips on promargin and one bicuspid tooth on retromargin. Palp with a straight embolus and a bifid RTA (Figs. 2–3). Sternum pale yellow. Legs light brown. No bulbous setae on tibiae I, but with a longitudinal row with seven small setae prolaterally on femur I. Length of femur I 1.20, II 1.10, III 1.05, IV 0.65; patella + tibia I 1.60, II 1.40, III 1.15, IV 0.90; metatarsus + tarsus I 1.00, II 0.95, III 1.05, IV 1.25. Spination (poorly preserved): femur I d1?, p1di; II d1-1?, p1di; III d1?, p2di, r1di; IV? ; patella I, II 0; III r1; IV 0; tibia I v2di; II 0; III, IV r1-1; metatarsus I v2-2; II v1r-2; III p2di,



Figures 1–5.—*Cotinusa furcifera* (Schenkel 1953): 1. Dorsal view of male; 2. Male palp, ventral view; 3. Male palp, retrolateral view. *Freya infuscata* (F.O. Pickard-Cambridge 1901): 4. Epigynum, ventral view; 5. Dorsal. Scale line = 2.0 mm (Fig. 1); = 0.5 mm (Figs. 2–5).

r1-1di, v1rdi; IV p2di, r1di, v1pdi. Abdomen (Fig. 1) pale yellow, light brown laterally.

Comments.—Since the genus has never been revised, we decline to speculate on the validity of this nominal species.

Distribution.—Known only from Venezuela (Platnick 2006).

Genus *Freya* C.L. Koch 1850
Freya infuscata
(F.O. Pickard-Cambridge 1901)
Figs. 4–5

Cyrene infuscata F.O. Pickard-Cambridge 1901: 235, pl. 19, fig. 14 [female holotype from Bugaba (8°28′N, 82°37′W), Provincia de Chiriqui, Panama, Champion (Natural History Museum, London), not examined].

Freya infuscata (F.O. Pickard-Cambridge): Petrunkevitch 1911:653; Kraus 1955:61, fig. 173; Platnick 2006.

Menemerus falconensis Schenkel 1953:49, fig. 43. NEW SYNONYMY.

Material examined.—VENEZUELA: *Falcón*: 2 female syntypes, El Pozón, Distrito Acosta (12°06′N, 70°00′W), October 1924–January 1925, K. Widenmeyer (NMB 2259-a).

Description.—Total length: 10.40. Carapace brown, 3.95 long, 2.85 wide, 1.95 high. Ocular quadrangle dark brown, 1.85 long, black rings

around eyes. Anterior eye row 2.55 wide, posterior 2.55 wide. Chelicerae dark brown, with two teeth on promargin and one on retromargin. Sternum light brown. Legs light brown, dark brown proximally and distally. Length of femur I 2.20, II? (leg absent), III 2.70, IV 2.40; patella + tibia I 2.80, II?, III 2.60, IV 2.90; metatarsus + tarsus I 1.80, II?, III 2.50, IV 2.75. Spination (variation in parentheses): femur I d1-1-1, p2di; II?; III d1-1-1, p2di, r1di; IV d1-1-1, r1di; patella I 0; II? ; III, IV p1, r1; tibia I v2-2-1p-2; II?; III, IV p1-1-1, r1-1-1, v1p-0-2; metatarsus I v2-2; II?; III p1-0-2, r1-1-2, v2-2; IV p1-1-2, r2-1-2 (r1-1-2), v2-2. Abdomen pale yellow, variegated with brown. Epigynal plate with two circular openings and spherical spermathecae (Figs. 4–5). Spinnerets light brown.

Comments.—Synonymy based on illustrations by F.O. Pickard-Cambridge and Kraus. The genus has not been entirely revised and therefore we cannot present a comparative diagnosis for this species.

Distribution.—Known from El Salvador, Panama and Venezuela (Platnick 2006).

Freya perelegans Simon 1902

Freya perelegans Simon 1902:414 [male lectotype from Caracas (10°30′N, 66°55′W), Distrito Federal, Venezuela, E. Simon, designated by Galiano (1963b) (Muséum National d'Histoire Naturelle, Paris), not examined]; Galiano 1963b:359, pl. XX, figs. 8–9; Platnick 2006.

Phiale albovittata Schenkel 1953:51, figs. 45a–b. NEW SYNONYMY.

Material examined.—VENEZUELA: *Falcón*: male holotype, El Pozón, Distrito Acosta (12°06′N, 70°00′W), October 1924–January 1925, K. Widenmeyer (NMB 2254).

Description.—See Galiano (1963b).

Comments.—Synonymy based on illustrations by Galiano (1963b). Only one (different) species group of this genus has been revised (Galiano 2001) and therefore we cannot present a comparative diagnosis for this species.

Distribution.—Known only from Venezuela (Platnick 2006).

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SHORT COMMUNICATION

THE SPIDER *ENOPLOCTENUS CYCLOTHORAX* (ARANEAE, CTENIDAE) AVOIDS PREYING ON THE HARVESTMAN *MISCHONYX CUSPIDATUS* (OPILIONES, GONYLEPTIDAE)

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ABSTRACT. Field observations suggested that the spider *Enoploctenus cyclothorax* (Bertkau 1880) avoids preying on the harvestman *Mischonyx cuspidatus* (Roewer 1913). The objectives of this study were to test the degree to which this prey avoidance occurred, and to test the effects of starvation on predation rates. Laboratory prey-predator encounters showed that 77.8% of the spiders rejected the harvestmen even after severe starvation, dying after sharing the same terrarium with a harvestman for 68.6 ± 21.8 days. Two spiders fed on the harvestmen, but only after one week. In comparison, crickets given to the control group were all consumed after 13 hours. Prey recognition and subsequent avoidance, without conspicuous exudation of the scent glands (92.9% of the cases), occurred only after the harvestman was touched. We conclude that adult *E. cyclothorax* do avoid preying on *M. cuspidatus*, even after severe starvation, suggesting that the latter is recognized by the former by its chemical properties.

Keywords: Opiliones, Ctenidae, prey avoidance, prey detection, distasteful

Spiders of the family Ctenidae are medium to large wandering spiders that typically inhabit forests (Gasnier & Höfer 2001). They hide during the day in natural retreats including holes in tree trunks and under the base of strong and large leaves of bromeliads, palms and others (Barth et al. 1988; Höfer et al. 1994). At night, they leave their retreats and wait for prey (Salvestrini & Gasnier 2001), which includes a large variety of arthropods (Barth & Seyfarth 1979; Höfer et al. 1994). However, ctenid spiders as a whole apparently do not feed on every prey they are able to subdue (see Nentwig 1986). Willemart and Kaneto (2004) observed adult female *Enoploctenus cyclothorax* (Bertkau 1880) attacking the laniatorid harvestman *Discocyrtus* sp. (Opiliones, Gonyleptidae) but moving back without biting after touching it with their first legs, even though the harvestmen never reacted aggressively. If *E. cyclothorax* actually avoids preying on a harvestman species, the latter could be added in the list of arthropods rejected by many spiders, such as some species of stinkbugs, ants, caterpillars and others (Foelix 1996). This study aimed to determine if adult *E. cyclothorax* avoids preying on a co-occurring harvestman and whether this prey avoidance behavior is associated with food deprivation (see Gelperin 1968).

Eighteen adult females of *E. cyclothorax* (length [total/cephalothorax]: ~ 20.0/9.0 mm), nine adult males of the harvestman *Mischonyx cuspidatus* (Roewer 1913) (dorsal scute length: ~ 5 mm) and nine adults of *Endecous betariensis* crickets (Phalangopsidae) (body length: ~ 15.0 mm) were used in the experiments. The spiders and the harvestmen were collected at night, in the Reserva da Cidade Universitária Armando de Salles Oliveira (C.U.A.S.O.), city of São Paulo (state of São Paulo), southeastern Brazil (23°33′S, 46°43′W), a well developed secondary forest. The crickets were collected in the Parque Estadual Turístico do Alto do Ribeira (PETAR), an Atlantic forest reservation in São Paulo state, southeastern Brazil (cave location: 24°32′57″S, 48°43′15″W), and were brought to the laboratory in vials. The crickets were transferred from the latter directly to the "cricket group" terrarium (see below). Voucher specimens were deposited at the Museu de Zoologia da Universidade de São Paulo (MZUSP).

Spiders were individually housed in clear plastic containers (20 l × 10 w × 10 h, cm) with damp soil on the bottom, and maintained at 25° C. In the first experiment, spiders were fed to satiation for 8–10 days (d) before the starvation period started by offering immature laboratory reared cockroaches

(*Periplaneta americana*, Blattidae) and adult laboratory reared crickets (*Gryllus gryllus*, Gryllidae) *ad libitum*. Harvestmen were fed on larval pieces of the beetle *Tenebrio molitor* (Tenebrionidae), boiled rice and water soaked bread and maintained in another laboratory where temperature was not controlled. *Endecous betariensis* crickets have been used as a comparison group in the experiment of prey-predator encounter. It was chosen for being a different species from the cricket used to feed the spiders, thus avoiding prey species recognition that could possibly influence the capture rate (see discussion in Curio 1976).

Nine spiders were randomly chosen to be tested with crickets and the other nine to be tested with harvestmen. Both groups were deprived of food 21 d before testing to maximize the possibility that they would be hungry. During the night period at 25° C in a darkened room, each spider of the "cricket group" was offered one *E. betariensis* cricket, whereas each spider of the "harvestman group" was offered one *M. cuspidatus* harvestman. Crickets and harvestmen were introduced in the terraria where the spiders were being maintained. Prey was placed as far from the spider as possible to create a more realistic situation in which the latter could detect the prey from a distance. We observed the spiders continuously during one hour, all at the same time (two observers; no predation events occurred simultaneously). In the following days, we checked whether the spiders preyed on the harvestmen/crickets once each 1–2 d, between 11:00 and 15:00 h, until either the harvestmen/crickets were eaten or the spiders died. As there were no retreats in the terraria, the prey could not hide from the spiders. Once a week, we fed the harvestmen (in the spider's terraria), with soaked bread or rice, items chosen because they would probably not be of interest to the spiders. These items were introduced in front of the harvestmen (< 1 cm away), thus allowing immediate feeding, and removed the following day to avoid fungal proliferation.

While checking the tested individuals every 1–2 d, we noted the position of prey and predators. Because the cover of the terrarium was divided by grids into six equal parts, we could conduct two analyses to infer mobility of both spiders and harvestmen in each terrarium (moving would facilitate mutual perception and therefore predation—see Barth 1982). We counted how many times each individual was in each section of grid, and how many times they moved from one part to another.

In a second experiment we investigated the physical interactions between spiders and harvestmen by conducting prey-predator encounters. Eleven adult or subadult *M. cupidatus* (5 females and 6 males) and 11 adult females *E. cyclothorax* were collected in the C.U.A.S.O. and brought to the laboratory. Spiders were maintained in the same conditions

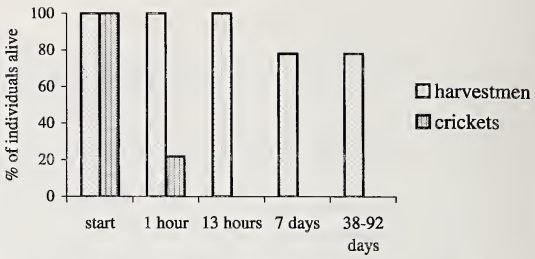

Figure 1.—Comparative predation rate by adult spiders *Enoploctenus cyclothorax* on the harvestmen *Mischonyx cuspidatus* and the crickets *Endecous betariensis*. The x-axis is time after the start of the tests.

mentioned above and deprived of food 21 d before each of the harvestmen were introduced in a spider terrarium, also as described above. We monitored each pair (the spider and the harvestman of each terrarium) continuously, at the same time (two observers, no predation events occurred simultaneously), until all the pairs had made physical contact and shortly thereafter. Our intention was to better describe at what point the spider avoided the harvestman (before or after contact), whether or not the spiders bit, and the harvestmen's defensive behavior. Data are presented as means ± standard deviation.

Within the first hour of the first experiment, seven out of nine crickets were consumed, and none of the harvestmen were preyed upon (Fisher exact test: $P = 0.002$) (Fig. 1). After 13 h from the beginning of the experiment, all crickets were eaten. Only after 7 d were the first two harvestmen eaten (i.e., 28 d after the spiders had last eaten [Fig. 1]). The two spiders that fed on the two harvestmen were kept in the terrarium, fed on *G. gryllus* once per week but died 11 and 33 d after eating the harvestmen (i.e., 18 and 40 d after the introduction of the harvestmen in their terraria). The other seven spiders kept with harvestmen without consuming them died 68.6 ± 21.8 d ($n = 7$; range = 38–92 d) after the harvestmen were introduced in their terraria (Fig. 1). After the first day of the experiment, spiders of the "cricket" group (which ate one *E. betariensis* and then one *G. gryllus* per week) died after 57.3 ± 28.6 d ($n = 6$; range: 14–95 d). There was no difference between the survival of spiders of the "harvestmen group" that did not consume the harvestmen and spiders of the "cricket group" (t-test: $t = 0.804$; $P = 0.438$; $df = 11$).

Both the harvestmen and the spiders were seen in almost all parts of the terraria and did move between these parts (changes from one of the six parts to another, in percentage of observations: spiders 66.4 ± 10.5%; harvestmen: 46.7 ± 7.6%), and so we assumed they perceived each other (Fig. 2).

Below we present data from the 11 observations

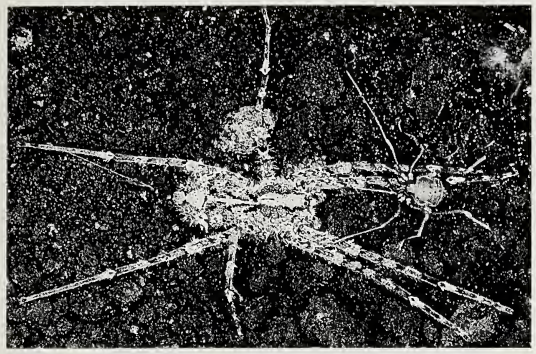

Figure 2.—An adult spider *Enoploctenus cyclothorax* showing no interest in the harvestman *Mischonyx cuspidatus*. Spider total length (cephalothorax + abdomen = ~ 2 cm). Picture by R. de Andrade.

of the second experiment plus three observations done with the "harvestman group" in the first experiment. In ten out of 11 observations, the spiders touched the dorsum of the harvestmen (with the ventral parts of their legs I and/or II and/or III and/or dorsum of the pedipalps) but retreated upon contact. Once, a spider gently carried a male harvestman forming a basket with legs I and pedipalps, then touched it with the mouth without biting, and finally released the prey. In another occasion the spider touched the harvestman's body with leg I, then bit its leg II and retreated thereafter. Once, a spider attacked the harvestman from a 5 cm distance (tip of the spider leg to the harvestman's body), but the harvestman managed to flee by running. No further contact was made.

In these 13 observations, the harvestmen did not release visible secretions from their scent glands and either remained motionless (n = 10) or kept walking slowly when contacted by the spiders (n = 3).

In only one case did the spider bite the harvestman's body. The spider gently carried the harvestmen with legs I and the pedipalps and bit the anterior region of its body. After holding it for three seconds, the spider released the harvestman and rubbed the dorsal region of her pedipalps and the anterior region of the body on the ground. At some point the harvestman released secretions from its scent glands since a characteristic odor spread out of the terrarium. Both the harvestman and the spider lived at least 30 d after the encounter.

The choice of prey by predators is expected to involve energetic values of prey, manipulation time (Elner & Hughes 1978; but see also Meire & Ervynck 1986), searching time (Krebs et al. 1977), and palatability (Eisner 1970). In turn, prey have developed several mechanisms used to deter predators, be they morphological, behavioral, chemical, or a combination of these features (see Edmunds 1974). There is no reason to believe that harvestmen provide so much less energy that it would not be worth to feeding on them after a long starvation period as other harvestmen are preyed on by several other organisms including spiders (see e.g., Machado et al. 2005). The harvestmen never used mechanical defenses that would require the need of any specific manipulation. Because ctenid spiders bear strong chelicerae, we also have no reason to believe that they would have to manipulate the prey to search for softer parts of the cuticle. Moreover, Willemart & Kaneto (2004) reported two individuals of *E. cyclothorax* feeding on two distinct harvestmen, which were left in pieces. Finally, searching time was minimal in our experiment. Both the spiders and the harvestmen moved in the small terrarium (Fig. 2) and there were no possible hiding places. Therefore, we must look for other reasons that would cause *M. cuspidatus* to be avoided by adult *E. cyclothorax*.

One possibility is that mechanical defense, such as bites with the chelicerae, pinching with the spiny pedipalps, or nippings with the fourth pair of legs (e.g., Gnaspini & Cavalheiro 1998) of the harvestmen inhibit attack by the spider. However, none of these behaviors were observed when the spiders touched, carried, or bit the harvestmen (as also observed by Willemart & Kaneto 2004). The possibility that rapid movement by the harvestman prevented the spiders from catching this prey can be empirically rejected since this rapid avoidance by the harvestman was only observed once in 12 observations, and in an exceptional case in which the spider did not wait for a closer range attack. We are left with the possibility of unpalatability, that a chemical defense provokes the rejection by the spider. Acosta et al. (1993) reported a thin and hardly detectable layer of scent gland secretions in the lateral grooves of resting *Pachyloidellus goliath* (Acosta 1993). This could result from release of small amounts of secretion or could be residual from previous exudations; either way it is possible that visually inconspicuous repellents were secreted by the test harvestmen in this study. Another possibility is that the tegument contains chemicals that are repellent to some predators (see Eisner et al. 2004; Machado et al. 2005). Therefore, even when no visible secretions are released, harvestmen may be chemically protected.

Because, in 13 observations, the spiders moved over the harvestmen and retreated only after touching them, we can infer that, although detection of the harvestmen occurred at a distance, recognition and rejection were only possible after contact. As discussed above, the chemical properties of the harvestmen, and not mechanical ones (such as size and texture), are probably mediating this recognition, since the former is more specific than the latter (see

Van Loon & Dicke 2001). Chemical recognition would be mediated by contact chemoreceptive hair sensilla, which are typically present mainly on the distal parts of the legs and pedipalps (e.g., Barth 2002).

Because of the small number of observations, we cannot speculate on why the two spiders that ate the harvestmen died sooner. Finally, we should note that feeding on crickets or not feeding at all did not result in differences in survival times among spiders, suggesting that death was not related to starvation and thus the latter did not play a role in increasing a spider's likelihood of consuming a harvestman.

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SHORT COMMUNICATION

HEAVY METALS IN CUTICULAR STRUCTURES OF PALPIGRADI, RICINULEI, AND SCHIZOMIDA (ARACHNIDA)

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ABSTRACT. Samples from Palpigradi, Ricinulei, and Schizomida were examined by energy dispersive X-ray spectroscopy (EDS) for the presence of metallic elements in cuticular structures. Manganese was found in Ricinulei while zinc was found in Palpigradi and Schizomida. When presence or absence of zinc is superimposed on a cladogram of arachnid orders, its absence in the Acaromorpha (Acari + Ricinulei) appears to be a derived condition. Similarly the absence of manganese in the Uropygi (Schizomida + Thelyphonida) may be synapomorphic as well.

Keywords: EDS, manganese, zinc

The presence of heavy metals in arthropod cuticular structures was first demonstrated by Hillerton et al. (1982) and Hillerton & Vincent (1982) in insects. How these metals are bound within the cuticle is still not known, although the specialized regions containing them are characterized by increased hardness (Hillerton et al. 1982; Schofield 2001). Heavy metals in arachnid cuticle was first investigated by Schofield & Levere (1989) and Schofield et al. (1989). In six spider species of four families (Araneidae, Lycosidae, Theraphosidae, Theridiidae), they found zinc in distal regions of fangs, and manganese in cheliceral teeth and tarsal claws. In two scorpion species from two families (Buthidae, Vaejovidae), they found manganese and zinc in cheliceral teeth in both species and iron in the buthid tissue as well. Schofield (2001) summarized results of examination of representatives of all arachnid orders except the Palpigradi, Ricinulei and Schizomida in an extensive table listing heavy metal occurrences in mechanical structures of animals. In addition to cheliceral structures he examined telsons and leg elements.

In the present paper we report on our examination of cuticular heavy metal elements of the three orders not included in the earlier studies:

Palpigradi (Prokoeneniidae)—*Prokoenenia wheeleri* (Rucker 1901), immature; USA: *Texas*: Travis Co., Lake Travis (30°25′N, 98°00′W), 24 July 2004.

Ricinulei (Ricinoididae)—*Pseudocellus* cf. *pelaezi* (Gutiérrez 1970), female; MEXICO: *Tamaulipas*: between kilo posts 4 and 5 off Highway 85 to Gomez Farias (23°02′N, 98°00′W), 16 May 2001.

Schizomida (Hubbardiidae)—*Stenochrus mexicanus* (Rowland 1971), female; MEXICO: *Tamaulipas*: between kilo posts 4 and 5 off Highway 85 to Gomez Farias (23°02′N, 98°00′W), 16 May 2001.

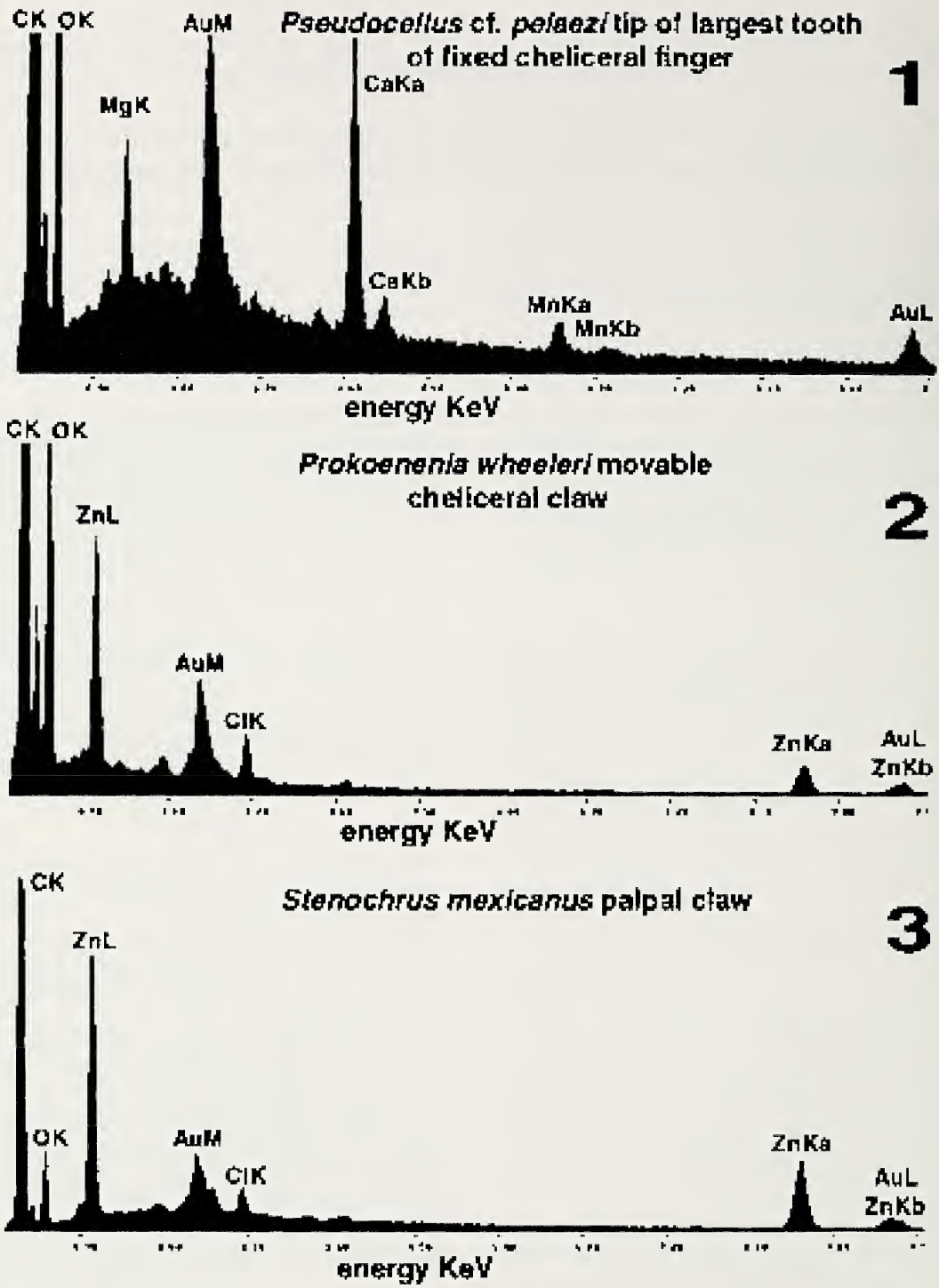
Structures analyzed were:

Prokoenenia—cheliceral body, movable finger, fixed finger, fourth tooth from distal end of fixed finger; leg 1 and 3 tarsal claws.

Pseudocellus—cucullus, cheliceral body, movable finger, fixed finger, largest tooth of fixed finger; palpal fixed finger, largest tooth of fixed finger; leg 1 and 4 tarsal claws.

Stenochrus—cheliceral body, movable finger, fixed finger; palpal tarsal claw, tarsal spur distal and proximal; leg 2 and 3 tarsal claws.

Specimens, collected by L. McCutchen and preserved in 70% ethanol, were dissected in fresh 80% ethanol and thus destroyed during processing. The parts were placed in 95% ethanol for 3 × 30 min, then 5 × 30 min in acetone, air dried out of acetone and mounted on SEM stubs with conductive carbon tabs and carbon paint. After being mounted, they were sputter coated with 10 nm of gold. Gold was chosen over carbon as a conductive coating, because of its superior electrical conductivity compared to carbon. The only problem encountered in relation to the elements of interest was the interference overlap of the gold La peak (9.71 keV) with the zinc Kb peak (9.57 keV). However, the zinc Ka



Figures 1–3.—Representative EDS spectra, non-background corrected, major elemental peaks are identified, the small peak between CK and OK is NK. Peaks are labeled by their elemental symbol and emitted X-ray type. 1. *Pseudocellus* tip of largest tooth of fixed cheliceral finger. MnKa peak (213 counts) at 5.90 KeV, MnKb peak (83 counts) at 6.49 KeV; 2. *Prokoenenia* tip of moveable cheliceral claw, ZnKa peak (617 counts) at 8.63 KeV, ZnLa peak (4960 counts) at 1.01 KeV; 3. *Stenochrus* tip of palpal claw, ZnKa peak (1077 counts) at 8.63 KeV, ZnLa peak (4213 counts) at 1.01 KeV.

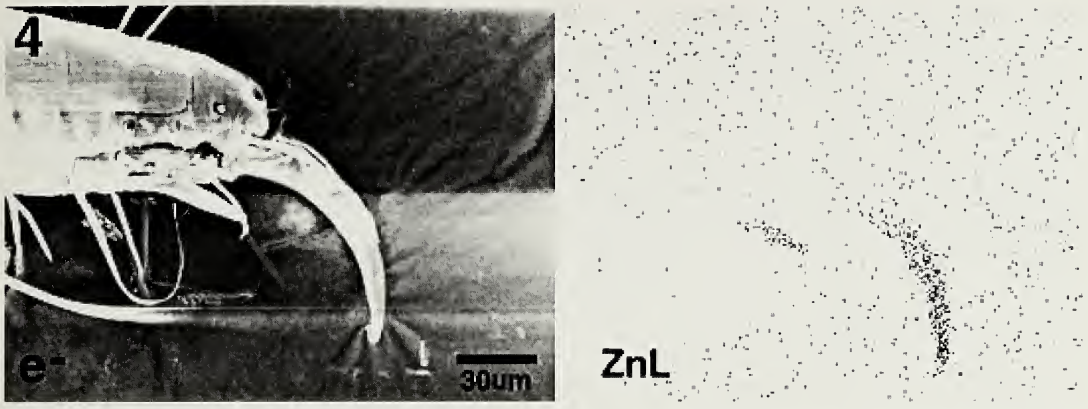


Figure 4.—Mapping of ZnL x-rays in the distal tarsal region of the palpus of *Stenochrus*. e⁻ is the secondary electron image (conventional SEM image, left) scanned at the same rate as the ZnL family x-ray map (ZnL, right). Note increased density of ZnL family pixels in the distal part of the tarsal spur and the claw. Original dimensions = 1024 × 800 pixels.

peak can be confirmed by the high zinc La peak (1.01 keV) in the same spectra.

Specimens were analyzed in a LEO 1550 field emission scanning electron microscope (SEM); equipped with an EDAX energy dispersive x-ray system (EDS), with an ultra-thin window Phoenix detector using Genesis software. All spectra were collected by focusing the electron beam at the tip of the structure except for the cheliceral body spectra which were collected from the center of the dorsal side in *Prokoeninia* and *Stenochrus*, and the center of the ventral side in *Pseudocellus*. Excitation voltage was 20 KeV and the working distance was 8 mm. Collecting times were 300–400 counting seconds. Beam current was measured using a Faraday cup. For the standard aperture used (30 μm) current was 245 pA, for the *Pseudocellus* cucullus a 60 μm aperture was used, current was 1.06 nA; for the *Pseudocellus* cheliceral body a 20 μm aperture was used, current was 111 pA. Major X-ray peaks were considered as positive when they had a minimum detectable level (MDL) of 99.9% certainty, MDL > background + 3 (square root of background) (Lee 1993).

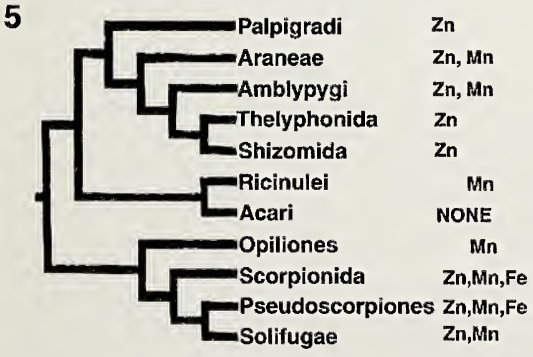


Figure 5.—Phylogeny of Arachnida based on Shultz (1990) with presence of cuticular metallic elements added. Palpigradi, Ricinulei, Schizomida from this paper, all others from Schofield (2001).

Zinc was detected in leg and palpal claws and distal cheliceral areas of *P. wheeleri* and *S. mexicanus*. Manganese was detected in one of the cheliceral teeth of *P.* cf. *pelaezi*. Calcium peaks are often associated with manganese peaks in arachnids as seen in Fig.1. In *P.* cf. *pelaezi* a magnesium peak often appeared with the calcium peaks whether associated with manganese or not. Representative spectra are shown in Figs. 1–3 while Fig. 4 shows an x-ray map of the distal palpal tarsus in *S. mexicanus*.

Energy dispersive x-ray spectroscopy (EDS) results in biological materials are considered to be qualitative because of the uncertain composition and heterogeneity of the materials being examined. Schofield and collaborators utilized particle induced x-ray emission (PIXE) and scanning transmission ion microscopy (STIM), which allow deep or complete penetration of the specimen. Using tomography based on these methods, one can achieve quantitative elemental results as well as deep element mapping. The disadvantage of using these methods is the limited availability of the instrumentation. Despite its qualitative nature in biology, EDS has the advantage of being far more available since many SEMs have EDS detectors installed for use in the geological and materials sciences. Qualitative results in EDS are readily attained in a short time frame making it an ideal surveying tool.

This study adds cuticular metallic element data for the three arachnid orders not included in Schofield's (2001) summary. When the distribution of the elements is superimposed on the cladogram of

Shultz (1990) (Fig. 5), the near ubiquity of zinc is obvious. Absence of zinc in the cuticle of Acaromorpha (Acari and Ricinulei) may be a synapomorphy of these orders. Similarly the absence of manganese in the Uropygi (Schizomida and Thelyphonida) may be synapomorphic as well. Absence of cuticular zinc may be a derived condition in Opiliones. However, both the Acari (two species in Schofield (2001), one by B. Cutler unpublished) and the Opiliones (three species in Schofield (2001), two by B. Cutler unpublished) have been very poorly sampled relative to the size of the orders. These orders should be investigated more thoroughly to check for the presence of zinc. Likewise, the lack of iron in the Solifugae (two species investigated, Schofield (2001)) indicates that a wider range of taxa within this order should be examined given its close relationship to Scorpionida and Pseudoscorpiones.

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Contents continued on inside back cover